

PREHISTORIC DISTURBANCE OF VEGETATION IN THE
AREA OF LAKE YAXHA, PETEN, GUATEMALA

BY

HAGUE HINGSTON VAUGHAN

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1979

ACKNOWLEDGEMENTS

It is a privilege to acknowledge with a profound sense of gratitude the guidance of Dr. E.S. Deevey whose patience and influence I can never hope to fully repay and, equally, my parents who, while perhaps never fully understanding what I was attempting to do much less why I was doing it, never failed to give me their complete support based solely on my opinion that it was worth doing.

This research was supported by a graduate assistantship in the Florida State Museum and from National Science Foundation Grants GB 32150 and BMS 72 01859 to Dr. E.S. Deevey.

PREFACE

The project "Historical Ecology of the Maya Area" of which this work is a part, was begun in 1972 under the directorship of Dr. E.S. Deevey of the Florida State Museum. The stated goals of the project were: (1) "to search the sedimentary record for evidence of Maya land use"; (2) "to evaluate human population densities and 'agro-engineering' activities during Classic and Post-classic time"; (3) "to learn enough of the special limnology and archeology to evaluate the record of air-borne and water-borne substances"; and (4) "to evaluate the basin-wide budgets of water, silicates and major anions and cations at present day and (by inference from chemical paleolimnology) as they were modified by Maya exploitation" (Deevey, 1973, quoted with permission of the Director from a proposal for renewal of research support, National Sciences Foundation Grant GB 32150).

This dissertation reports the contribution made towards achieving these goals by the stratigraphic analysis of the plant macrofossils and pollen in the lacustrine sediments of the lake district in The Petén, Guatemala.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
PREFACE	iii
LIST OF FIGURES	v
ABSTRACT	vii
INTRODUCTION	1
THE MODERN ENVIRONMENT OF THE PETEN	6
Geology and Topography	7
Climate	8
Soils	11
Lakes and Hydrology	24
Vegetation	29
LOCAL MAYAN POPULATIONS	43
MESOAMERICAN AND SUBTROPICAL PALEOECOLOGY	56
CONSIDERATIONS FOR TROPICAL PALYNOLOGY	69
METHODS	74
RESULTS	79
DISCUSSION	111
SUMMARY	140
LITERATURE CITED	152
APPENDIX A INITIAL ANALYSES OF LAKE QUEXIL CORE 1 PERFORMED BY G. H. YEZDANI AND H. VAUGHAN	162
APPENDIX B EXAMPLE CALCULATIONS	173
BIOGRAPHICAL SKETCH	176

LIST OF FIGURES

Text

1: The Lakes Area, Petén, Guatemala	19
2: Bathymetric Map: Lakes Yaxha and Sacnab	21
3: Bathymetric Map: Lake Quexil	23
4: Lake Sacnab Core 1: Physical Stratigraphy and Loss on Ignition	98
5: Lake Quexil Core 1: Relative Pollen Diagram	100
6: Lake Sacnab Core 1: Relative Pollen Diagram	102
7: Lake Quexil Core 1: Carbonized Fragments, Urticales Complexity and Initial Approximation of Pollen Influx .	104
8: Lake Quexil Core 1: Physical and Chemical Stratigraphy, Derivation of Depth/Age and Sedimentation Rates	106
9: Lake Quexil Core 1: Total Pollen and Carbonized Fragment Influx	108
Lake Sacnab Core 1: Carbonized Fragment Influx	108
10: Lake Quexil Core 1: Pollen Influx Diagram	110
Appendix A: Initial Analysis of Lake Quexil Core 1 Performed By G.H. Yezdani and H. Vaughan.	
11: Lake Quexil Core 1: Relative Pollen Diagram: Arboreal .	162
12: Lake Quexil Core 1: Relative Pollen Diagram: Nonarboreal	164

13:	Lake Quexil Core 1: Sponge Spicule and Rhizopod Density .	166
14:	Lake Quexil Core 1: Phytoplankton Density	168
15:	Lake Quexil Core 1: Zooplankton Density	170
16:	Lake Quexil Core 1: Plant Tissue, Carbonized Fragment and Fungal Element Density	172

Abstract of Dissertation Presented to the Graduate Council
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

PREHISTORIC DISTURBANCE OF VEGETATION IN THE
AREA OF LAKE YAXHA, PETEN, GUATEMALA

By

Hague Hingston Vaughan

August 1979

Chairman: Dr. E.S. Deevey

Major Department: Zoology

Pollen and plant fossils in the Holocene sediments of northern Guatemalan Lakes Quexil and Sacnab were examined and related to what is known of Lowland Maya history, local population growth and distribution, climatic sequences in the lowland tropics and the nature of tropical vegetation. Located in the Petén, a low-lying karsted area with a warm, humid seasonal climate, semi-deciduous tropical forest, swampy bajos and savanna, both lake basins were subject to varying degrees of human disturbance from 5000 BP to the present. Archaeological investigations around Lakes Yaxha and Sacnab demonstrate exponential growth (0.17 per cent per year) of non-urban populations from Middle Preclassic to Classic times, reaching a density of 210.5 persons/km² prior to the Collapse. A nucleated Postclassic population of 5,000 persons was located on the islands of Topoxté in Lake Yaxha. Spanish conquest of the area took place in 1697.

Initial Analysis of the 9400 year record from Lake Quexil indicates extensive forest prior to the widespread savanna previously hypothesized to have been altered to a high forest by Mayan activities.

More intensive analysis using high magnification counting techniques, information derived from the carbonized plant fragments, sediment type, chemistry and aquatic fossils demonstrates a record of climatic and human disturbance. Percentage dominance by Urticales pollen make an influx diagram necessary. With the exception of the bottom-most date in Quexil, all ^{14}C dates are subject to an unknown and inconsistent degree of carbonate error. Dating control is therefore based on the established Mayan chronology.

Prior to human disturbance, local periods of humidity between 9400 and 7500 BP and 6500 and 5000 BP agree with the record found generally in the tropics. Earliest disturbance resulted in savannaization of the flat area of silty clay south of Lake Quexil. Modern bajo areas appear to have been occupied by a mosaic of ponds, banks and wet grasslands prior to the extensive clay erosion caused by the Maya, observed as thick clay layers dating from Classic and Postclassic times in the sediments of all lakes examined.

Disturbance of preferred upland areas under a more seasonal or drier climate than previously alters evergreen forest to Moraceae dominated semi-deciduous forest between 5000 and 3000 BP.

Between 3000 and 2000 BP, climate was highly seasonal with increasing between-year variability in either seasonality or total rainfall. Population growth forced use of less preferred areas resulting

in increasing savanna on flatter areas and possibly low deciduous forest on rolling areas. Land-use and vegetation increased in diversity over the area as both became increasingly specific to the features of any one site. General instability may contaminate interpretation.

Between 2000 and 1500 BP, seasonality decreased as did total rainfall resulting in low lake levels. Savanna reached its maximum extent. Rainfall increased at 1500 BP resulting in a climatic pattern which has persisted to today except for occasional incidents of lower rainfall and lake levels.

Between 1500 and 1070 BP all areas were subject to increasingly permanent use. Deforestation was almost total in the Quexil basin, less so near Sacnab. Savanna declines due to exploitation or physical occupation.

Postcollapse population dispersal was gradual in these non-urban areas as opposed to the apparent suddenness observed in urban areas. Small residual populations were present in both basins as some reforestation took place. Nucleated Postclassic disturbance indicates a level of land-use intensity comparable to that of Classic populations. Reforestation of the area following dispersal took 150 years. Savanna has been re-established near Lake Quexil during the past century.

The climatic record resembles that for other tropical areas but further comparable records from other Mesoamerican areas are needed to establish the meaning of its variations and the magnitude of change.

INTRODUCTION

The aura of mystery which surrounds present-day perception of the Mayan civilization is, to a great extent, due to the lowland tropical forest within which its remains are to be found.

Despite the strength of prevailing motivations, tropical forest areas persist in being under-developed and under-exploited relative to the efforts and technologies applied in overcoming the difficulties such areas present. In contrast, the Maya occupation of Petén, Guatemala and Belize from approximately 1000 BC to 900 AD represents one of the few examples of a society developing to a state level of social organization within the context of a tropical forest environment. Understanding of the manner in which this came about has been restricted by the destruction of Mayan records at the time of the Spanish conquest of Mesoamerica and by reforestation of the Maya area. To any observer of Mayan urban areas and temple structures presently overlain with dense vegetation, the relation between the Mayans and their environment would appear to dominate all other considerations.

While earlier emphasis was on the study of these urban areas, recent efforts have increasingly emphasized environmental effects in being directed at the study of the populations which surrounded and sustained them (Bullard 1960, Haviland 1965, 1969, 1972, Willey and Bullard 1965). In addition to clarifying the structure of Mayan society, such study has led to a greater appreciation of the size of the Mayan population: in connection with this project settlement surveys within

a large basin demonstrate an average population of approximately 250 persons per km² during Classic time. (Rice, 1976) The modern Petén, with the exception of settlement along the few roads and around the single string of lakes is almost uninhabited.

Fortunately, the remains of a civilization are not restricted to its art and architecture. Its past existence may also be seen in the present pattern of vegetation and soils but more important than these, its history and in particular, the history of its relation to its environment may be discerned in the plant fossils, animal fossils and chemistry of lake sediments. Deposited in discrete layers over time, the changing patterns of these record environmental history in a manner similar to the pages of a book. This dissertation, and indeed much of the project as a whole, may be considered as an attempt at interpretation of such a text.

While interesting in its own right, the object of such interpretation is not simply a reconstruction of history. The desired end is insight into the ecological processes of which such history is a product. A human society is not a system whose states and processes may logically be studied in isolation from its environment. The irreducible unit of study is one of which terrestrial, aquatic, climatic and human social systems are intimately interlocked components such that the states and processes of any one affect the others. Thus the history of any one component may only be truly understood by a knowledge of the parallel histories of the others with the result that questions of cause and effect become exceedingly complex. There is no lack of examples of this complexity in the literature pertaining to the processes of long-term vegetational, aquatic, climatic or social change

but one relevant example is the continuing debate concerning the cause of the Maya 'collapse' around 900 AD (Culbert 1973) which emerges as more of a product of these processes than of an isolated cause though such a cause, at present obscure, may have acted as a trigger.

The orientation of the project as a whole may be viewed as an experiment. In scientific analysis understanding of any system (the 'black box') is achieved by initial study, subsection of the system to a known treatment and analysis of the result. In terms of the design of the project, the Mayan presence may be considered as such a treatment.

The chosen site of the experiment is a pair of similar and adjacent lakes, Yaxha and Sacnab, differing, on initial examination, in the intensity of Maya occupation. Lake Yaxha supported both a Classic (Yaxha) and Post-classic (Topoxté) center while Lake Sacnab appears to have been lightly settled thus presenting a high and low intensity of 'treatment' which could be analyzed archeologically. The archeological results could be related to the history of change in terrestrial and aquatic systems as derived through paleoecological analysis of the sediment contents, the interpretation of which would depend on analysis of the present day ecology.

Drs. Donald and Prudence Rice of the Florida State Museum studied the Mayan populations in these basins by means of a settlement survey which relates the size and distribution of the population over time to present day topography, soils and vegetation (Rice 1976, Rice 1978, Rice and Rice in prep.). The modern vegetation was studied by Dr. J. Ewel and R. Myers of University of Florida to give greater

resolution to other more general published studies (Ewel and Myers 1974). Study of modern limnology, while concentrated on these two lakes, has concerned itself with other lakes in the area as well (Deevey, Brenner, Flannery and Yezdani in press, Deevey et al. in press, Deevey, Vaughan and Deevey 1977).

While it might be ideal to have complete studies of the sediments of Lakes Yaxha and Sacnab, paleoecological analysis is often limited by the quality of the sedimentary material, particularly in terms of the state of fossil preservation, as well as the ability to obtain samples from sufficient depth and of sufficient age. The sediments of Lake Yaxha thus far obtained have been less than ideal in both respects and this dissertation discusses the results from Lake Sacnab and Lake Quexil, some 45 km east of Yaxha and Sacnab where an 8400 ^{14}C year sedimentary record has been obtained. While no settlement survey work has been conducted in the Lake Quexil basin, this lack is compensated for by an increased ability to separate regional and local aspects of vegetational history by comparison of the two records. Comparison of the records from two adjacent lakes would yield little in this respect.

The analysis reported here is of the pollen and plant macrofossils contained in these sediments and their use in reconstructing the vegetational history of the area. These same sediments yield aquatic fossils whose analysis provides a parallel reconstruction of lacustrine history while the nature and chemistry of the sediments indicate in part the history of the relation between aquatic and terrestrial systems (Brenner 1978, Deevey 1978, Deevey et al. in press).

Insight into the processes within the system as a whole may be achieved through the heuristic framework which these reconstructions along with the archeology provide. Any hypothesis which, for example, explains the observed vegetational changes must be consistent with all other lines of evidence. In this manner a diversity of parallel stratigraphic histories may be used to restrict the potential interpretations by trial-and-error in addition to increasing the possible insight into cause and effect.

While this dissertation centers on the six parallel histories provided by the pollen, carbonized plant fragments and physical features of the sediments in the two lakes, information from the archeology, paleolimnology and sediment chemistry will be used as needed.

NOTE: This dissertation was written without the benefit of access to the splendid volume on Maya agriculture edited by P.D. Harrison and B.L. Turner. (Pre-Hispanic Maya Agriculture. Harrison and Turner (eds.). University of New Mexico Press, Albuquerque. 1978)

THE MODERN ENVIRONMENT OF THE PETEN

The Department of Petén, Guatemala presents a remarkable diversity of vegetation which is not readily apparent on casual observation. Though this study concentrates on the area surrounding the Petén string of lakes which occur in an east-west trending fault line at Lat. 17° N, the diversity found may be considered typical of the Petén as a whole. Locally, differences in topography, soils and drainage result in varying forms and composition of vegetation and this is modified by differences in climate to result in further vegetational variance over the entire Petén. While the distribution of many arboreal species is believed to be partially a product of their usefulness to the ancient Maya (Lundell 1937, Wagner 1964) the extent to which forms of vegetation such as savanna or bajo are a product of Maya activities is subject to debate (Lundell 1937, Tsukada 1966, Harrison 1977).

While this variation may also be observed in related faunal distributions, one of its more important results is that agricultural potentials will also vary. This feature could result in a diversity of increasingly specific strategies of exploitation under conditions of increasing population in a finite area.

Speculation on Mayan subsistence and agricultural strategies on the basis of modern observation (Cowgill 1961, Reina 1967) has, in consequence two major sources of difficulty. The first is that it is not known to what extent present types, distribution and agricultural

potential of vegetation differ from Maya times. Such difference could be due to differences in climate as well as the alterations in the environment Mayan activities produced.

The second is that modern agricultural methods in the area tend to reflect the conditions of low population density.

Geology and Topography

The central Petén is a low-lying (altitude 100-300 m) karst plateau between 16° and 18° north latitude composed of Cretaceous to Miocene dolomitic limestone overlying Tertiary marine clastics and limestone. Interbedded with evaporites, this limestone results in typical solution topography with sinkholes, caverns and underground streams (Viniegra, 1971, Vinson, 1962, West, 1964).

The southern Petén and the Maya mountains are composed of Mesozoic marine and continental sediments, Triassic shales and Cretaceous and Jurassic limestones (West, 1964) and were subject to activity within the Antillean orogenic belt resulting in a series of east-west oriented hills and faults. This activity is further seen in a general east-west orientation of the karst topography in the central Petén with occasional folds and ridges and a fault fracture at Lat. 17° north whose depressions have become the central Petén lake system.

The limestone contains siliceous nodules of chert and flint which provided material for Mayan tools while the limestone itself provided building and sculptural material. Solution downwasting of the limestone produces montmorillonitic clay as a residue and this clay fills the low-lying areas producing the impermeable soils which characterize the swampy bajos. It is possible that prior to accelerated clay

erosion and transport during the Mayan occupation, these bajo areas were shallow lakes (Harrison, 1977) although this idea is categorically rejected by Cowgill and Hutchinson (1963).

Climate

The climate of the Petén is warm and humid with a mean average annual temperature of 25.5°C and rainfall averaging 1600 mm only 5 to 10 per cent of which falls in the 5 months (January-May) of the dry season. The mean average temperature difference between the warmest and coolest months is only 6.7°C but diel air temperature difference is often wider.

The rainfall pattern results from the influence of the Northeast Trade Winds and humid tropical air masses. During the wet season (August-November) moisture laden Trade Winds are forced upward upon contacting the Equatorial Calms and therefore cool and lose their moisture. This effect is associated with the position of the sun and the thermal equator such that in the local dry season the rain belt has moved southward and local climate is a result of dry and cool air originating in higher latitudes (Vivo Escoto, 1964).

During the rainy season, the Trade Winds are not forced to rise as abruptly in the northern Petén as they are in the south and the result is that average annual rainfall generally increases as one moves from north to south in the Petén.

Within the limits of this general pattern atmospheric movements and their climatic effects can be quite complex. Vivo Escoto (1964) attributes this complexity largely to the position of Middle America

between the middle and low latitudes with their relatively simple air dynamics which combine and interact to affect Middle American climate. Tropical cyclones (hurricanes) of late summer and autumn and the invasion of cold northern air masses with weak frontal storms are quite unpredictable. There is also a short dry period of one or two weeks or even more during July or August called the veranillo which is due to a southward retreat of the equatorial calms.

Variations in either or both of the general weather patterns of middle or low latitudes may affect the climate of the Petén in more obscure ways which reflect the interdependence of climatic features and processes on a global scale. Namias (1963) shows that a strong sub-tropical high and resulting strong Northeast Trade Winds are associated with bands of above and below normal precipitation in Central and South America through enhanced rising motion in the Inter-Tropical Convergence Zone (ITCZ) and its possible southward displacement. The increased strength of circulation in the Hadley cell also results in poleward displacement of the upper level westerlies. Under the opposite conditions (weak sub-tropical high and Northeast Trade Winds) the precipitation bands reverse (i.e., areas above normal become below normal, etc.).

Extending and testing this concept, Namias (1972) demonstrated that the strength of the sub-tropical high is dependant on the degree of cyclonic activity or blocking in the Newfoundland-Greenland area during northern hemisphere winter and spring, strong cyclonic activity in this area being associated with a strong sub-tropical high while anti-cyclonic activity (blocking) is associated with weak or absent sub-tropical highs.

Because the vigour of the northern hemisphere general circulation is greatest during winter and spring and its large-amplitude long waves become a major feature of global circulation, this mechanism is found to affect precipitation patterns in low latitudes of the southern hemisphere where the ITCZ is then located by increased rising motion in the ITCZ causing increased vigour in the southern hemisphere Hadley cell (i.e., stronger Southeastern Trade Winds). Weather data for the southern hemisphere is relatively sparse so that the effects of southern hemisphere general circulation cannot be as well analyzed, but this argument would imply that precipitation patterns in the Petén during the rainy season might be strongly affected by a similar mechanism having as its basis activity in the southern hemisphere depression tracks. Such an hypothesis is strongly supported by the work of Maley (1973) who relates the lake levels of Lake Chad (14° N Lat.) during the last millennium to the activity of the Southern Polar Front in the southern hemisphere.

In consideration of the intricacy of world climate it would be indeed surprising if this were the only mechanism affecting climatic variability in the Petén and it is likewise difficult to assess the extent to which such a mechanism might dominate as a cause of such variability yet Namias' analysis makes a number of salient points. A major one is that world climate is a highly interlocked system and that alterations in local climate in the sub-tropics, being physically located at a major point of such interlocking, may be indicative of changes in the system as a whole.

Weather records for most of Central America are meagre and unreliable with the exception of those from some of the national capitals. Vivo Escoto (1964) estimates relative year-to-year variability in total rainfall in the Petén at under 20 per cent, although the areas of least rainfall variability when measured as a percentage are likely to be the areas of moderate to abundant precipitation. In terms of the impact of variability on vegetation and agriculture such a figure tells one very little.

A second form of variability is that of the relative year-to-year pattern of rainfall distribution which may differ appreciably especially in the months between the rainy and dry seasons (May-July, November-January). Records from Flores for 1971, a particularly dry year in the Petén, show that rainfall was especially lower from April through July though lower than normal in all months except August and October in which rainfall was approximately 50 per cent higher than normal and normal respectively.

The success of local milpa agricultur^e depends to a great extent on the successful prediction of the exact onset of the rainy season but this form of variability also affects the annual variation in lake levels and, in combination with total rainfall variability, the degree of deciduousness of forested areas and the frequency of grassland fires.

Soils

The observation that a given climate and its physiognomically correlated vegetation will produce a regional soil type is the basis for the concept of zonal soils. Local differences in topography,

hydrology, history and vegetation which are sufficiently extreme to give rise to variations on the major theme are the basis for intrazonal or azonal soils. This 'top down' scheme of description contrasts in part with the concept of the soil series in which higher order groupings are the results of similarities in local descriptions. The two points of view do not necessarily conflict yet the latter has proven far more satisfactory in tropical areas where a uniform climate may produce a great variety of soils exceeding in variability and quantity those found in a temperate area. The former method of classification which is a product of the development of soil classification in temperate areas and a traditional concern with agricultural potential reflects an assumption as to the constancy of the relative contribution made by the various factors in soil development and structure: localized differences in this relative contribution may thus be viewed as exceptional, e.g., topographical or hydrological extremes. In tropical areas local differences appear to be the rule rather than the exception and climate has relatively less effect on the development of soil characteristics.

The extent to which one differentiates between soil series gives rise to a concomitant differentiation of vegetation and the reverse is also true as a consequence of the dynamic interaction between soils and vegetation. Higher order groups of soils may be related to differences in topography and hydrology and ultimately all are subject to those processes of weathering which result from humid tropical climate and vegetation.

Simmons, Tarano and Pinto published a regional soil study of the Petén in 1959 which identified twenty-six different soil series on the basis of parent material, depth, drainage, texture and fertility which Stevens (1964) relates to form higher categories of soil classification. Nearly all the soils are derived from calcareous parent material, the exceptions being those in the extreme southern Petén near Lake Izabel.

High rainfall and temperature conditions give rise to extremely weathered soils through the process of laterization resulting in the zonal lateritic soils where topography is relatively flat. These soils are highly leached of mineral nutrients with the greater proportion of nutrients being in the vegetation or surface organic matter and with soil composition largely dominated by residual 2:1 clay minerals (montmorillonite, illite) and oxides. They generally have a good crumb structure due to the flocculating and cementing action of Al and Fe oxides and while this results in decreased erosion it also leads to higher rates of leaching. They are fairly acid due to the aluminum ions and this leads to the fixing of negative ions, particularly phosphorous on the positively charged oxides. Exploitation is often limited by low levels of mineral nitrogen which is highly mobile and easily leached. In some forested areas these soils may be initially productive but lose fertility rapidly once the forest cover is removed.

Lateritic soils are found in the southern and western Petén under forest and savanna but are found neither in the area of the Petén lakes nor to the north of them. Reddish-brown lateritic soil occupies a large area of savanna approximately 20 km south of Lake Petén-Itza

beyond a range of karst hills and there is some question as to whether this soil is a remnant of forested lateritic soil somewhat further leached and transformed following Mayan deforestation (Stevens, 1964: 299).

Soils in the area of the lakes form two major groups: the well drained lithosols, which are young soils with little horizon development, and the poorly drained Calcimorphic Rendzina and Hydromorphic soils which result from alteration in the normal role of water in soil development.

The general topography of the lakes area is such that their northern shores are bounded by a sharp range of hills or escarpments. A range of karst hills to the south of the lakes tends to run in a WSW to ENE direction such that lakes in the westerly end of the chain have their southern shores bounded by a gently rolling plain while those towards the east increasingly have hilly southern shores. To the north and north-east of the lakes, beyond the immediate hills, areas of hills and rolling plains alternate with low lying swampy areas (bajos) with deep poorly drained soils.

On moderate to steep slopes are found the Black Calcereous Lithosols (Cuxu, Jolja and Yaxha series) which are characteristically thin, well drained and fertile. These are young soils whose fertility is derived from the soft limestone parent material but which lack the crumb structure found in more highly weathered soils and are therefore easily eroded. The Brown Calcereous Lithosols are similar but found on harder limestones on the karst hills south of Lake Petén-Itza (Chacalte and Sacluc series).

The erodibility of these upland soils results in characteristics of the Calcimorphic Rendzina soils found on rolling areas and gentle slopes (Uaxactun and Macanché series). While shallow and poorly drained their fertility is constantly being renewed from upland areas and they are potentially the most productive soils in the area. Though the poor drainage limits nutrient leaching, they are sufficiently weathered for development of texture and structure with the result that they are not easily exhausted or eroded. Both these and the Lithosols support forest vegetation and Stevens (1964: 300) points out that most major Classic Maya ceremonial centers are located on or between these two soil groups.

The ultimate recipients of the products of upland erosion are the low lying bajo areas and this results in the deep poorly drained Hydromorphic soils found in these areas (Chapayal, Chocop and Yaloch series). These are composed of plastic clay with little horizon development and are subject to permanent or intermittent flooding. Of low to moderate fertility, they are extremely difficult to work agriculturally, rapidly depleted and require a long period of recovery. They support a variety of vegetation from swamp forest to wet grasslands according to the local degree of flooding and drainage. Such areas may be found to the east and north-east of Lake Sacnab and on the southern shore of Lake Yaxha but are rare in the basins of the lakes further west.

One exceptional soil of this type, however, is found in the area immediately south of Lake Quexil (Echixil series). While also being deep, poorly drained and of low fertility, it is of moderately friable

silty clay and presently supports a savanna, although this may be a result of recent human disturbance.

Stevens (1964: 302) is of the opinion that the modern lithosols may be undergoing rejuvenation after a former period when intensive cultivation and accelerated erosion removed a thicker and more productive soil. In many tropical karsted areas, the usual soil types found on upland and lowland areas are the Alfisols and Vertisols, the former being older and more weathered than lithosols and the Vertisols being more structured and less dominated by plastic clay than the Petén bajo soils. The present Petén soils would therefore appear to be a result of accelerated erosion altering the more usual juxtaposition.

Within these broad groups local soil differences occur in water-holding capacity, drainage, nutrient status and availability, soil texture, root room, profile characteristics and history which are reflected in vegetational differences.

Vegetation will in turn affect soil characteristics in a great many ways. In particular, differing areas of nutrient storage lead to changes in nutrient cycling, soil structure and, in affecting the soil PH, variations in the weathering processes. These are also affected by the variations in surface erosion and by shading which alters soil temperature, microbiological action and soil compaction from direct rainfall. Differences in soil microbiology are especially important under conditions of limited fertility not only in the breakdown of organic matter but also in nitrogen fixation by free-living bacteria such as Beijerinckia and Clostridium and host-specific Rhizobia. The nutrient accumulating actions of host-specific Mycorrhiza will further alter local nutrient cycling.

It is difficult to overstate the importance of the localized interactions between the physical and chemical features of the soil, soil microbiology and vegetation. Because of the nature of available tools paleoecology in general and pollen analysis in particular must deal with the nature of change on some generalized scale yet it must be remembered that such a scale is in many respects an artificial one being not so much a representation of reality as a function of these tools. Human and climatic disturbance of vegetation will be observed through pollen analysis as an average over the entire area yet their exact nature is obscured since the effects of such disturbance occur at the scale of these localized interactions.

In this respect, the taxonomy of regional soils in which the higher order groupings are due to shared qualities within a number of soil series which are attributable to the dominant forces in soil formation is the most reasonable framework for the interpretation of vegetational changes since such a taxonomy parallels and is related to vegetational differences. Any larger scale is too general to have much meaning and a smaller scale, however desirable, is not possible given the nature of the evidence.

Interpretational limits may be approached however during periods when the nature of human disturbance varies according to a finer scale. For example, if with an increasing population in finite space, exploitation strategies increasingly differ at the soil series level then interpretation based on a scale of higher order soil groupings may suffer by overgeneralization.

Figure 1: The Lakes Area, Petén, Guatemala

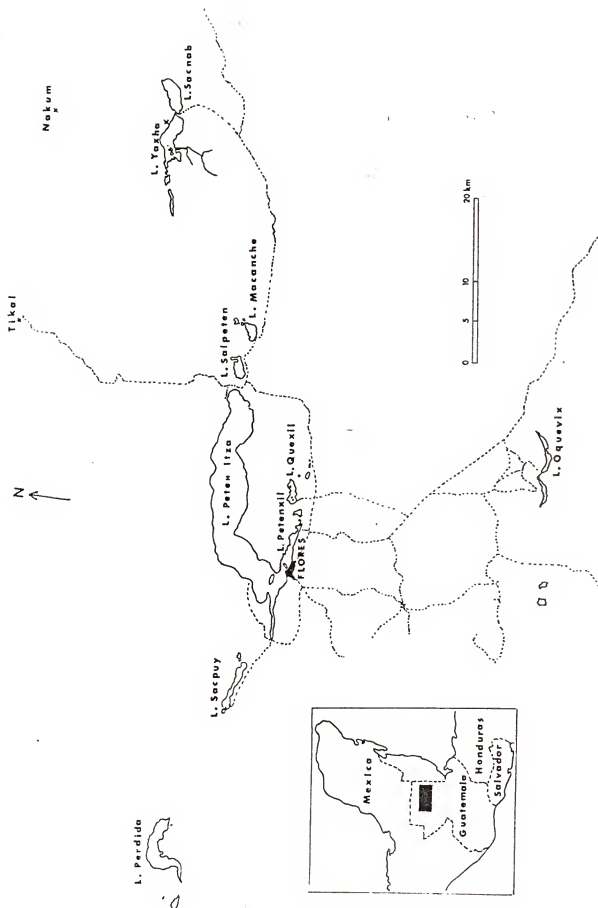


Figure 2: Bathymetric Map: Lakes Yaxha and Sacnab

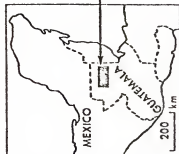
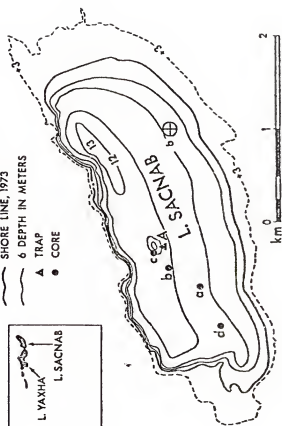
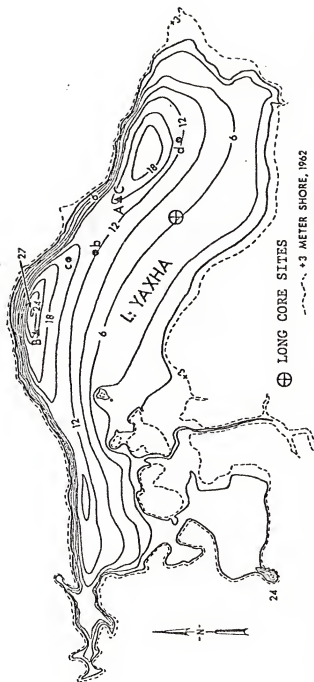
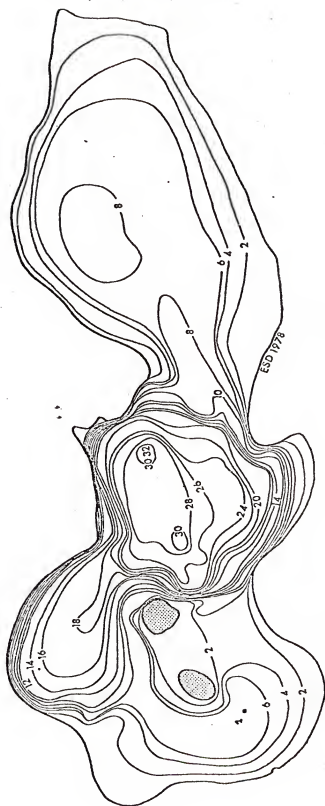


Figure 3: Bathymetric Map: Lake Quexil

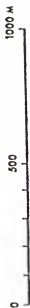
LAGUNA QUEXIL



• COAST



CONTOUR INTERVAL 2 M



SCALE

Lakes and Hydrology

Due to the porous limestone bedrock and the seasonal climate, surface drainage in the Petén is generally inconsistent with almost all streams and rivers containing running water only in the rainy season. Sinkholes, characteristic of karst topography are common as are aquadas in low-lying areas. Either may be sealed from the porous limestone by clay deposition and, depending on their depth, the thickness of such a seal and the relative position of the immediate water table, may contain water seasonally or throughout the year.

Swamps or bajos, are most common in the area of implied heaviest Mayan occupation and, as previously discussed, are characterized by thick impermeable clay soils. Bajos are intermittently flooded and, in most, at least the lower soil horizons may be permanently flooded. They are often found around seasonal streams though the location of the main channel(s) may shift in response to the dominant flow pattern during the period of flooding.

Lake Petén-Itza is the largest lake in the central Petén lake chain. Its main basin lies to the north with a smaller parallel southern basin separated from it by the Tayasal Peninsula and containing the island city of Flores. This subsidiary basin is continued to the east as Lake Peténxil (or Peténchil), Lake Quexil (or Eckixil, Exiquil), Lake Paxcamen and Lake Juleque. The main basin of Petén-Itza continues to the east as Lake Salpetén (or Sucpetén, Peténsuc), Lake Macanché, Lake Champoxte, Lake Yaxha and Lake Sacnab and to the west as lakes Picu, Sacpuy (or Seipuy) and El Sus (or El Zotz). These lakes together with a number of sinkholes and aquadas form the central

Petén lake chain located along the east-west fault line at Lat. 17° N. Further west, lakes Perdida and Larga follow the same axis but lie outside the actual fault line depression as do lakes Ija and Oquevix (or Pecay) which are shallow (approximately 1 1/2 m) twin lakes in the savanna area 30 km south of Lake Petén-Itza.

All of these lakes are of apparent internal drainage with inflowing seasonal streams and most are probably connected to groundwater through sinks which generally lie towards their northern shores. There are no apparent surface outlets and evaporation appears to be the dominant form of water loss. Their depths vary from very shallow to as much as 60 meters in Petén-Itza.

Lake Petén-Itza lies at an elevation of 110 meters, Peténxil lies 5 meters above Petén-Itza and Quexil 5.5 meters above Peténxil. Lakes Yaxha and Sacnab are at an elevation of 183 meters.

Though lake levels vary seasonally, the extent to which they vary over longer periods is an open question. In recent times the islands of Topoxté in Lake Yaxha which are at present attached to the mainland may be seen to be completely detached in 1963 air photos, indicating a rise of approximately 1 - 2 meters over present levels. Lakes Yaxha and Sacnab are known to have been connected over what is now a low isthmus at various times in their histories which would require a rise of 3 - 4 meters over present levels. Far more important to this study, however, are indications of levels in the more distant past in that extremes would have caused changes in the pattern of sedimentation as well as indicating climatic conditions.

All of these lake basins contain evidence of pre-Colombian occupation and the presence of ruins on many islands and peninsulas would indicate that lake levels were similar, or at any rate not higher, than at present during their construction and occupation. Frey Andrés de Avendano y Loyola travelling through the region in 1695-6 asked the local populace, the Itza, why they built their houses so close to the shores of Lake Petén-Itza and was told that the lake never rose or fell (Means 1917: 18).

Lundell (1937: 21) states that the level of Petén-Itza had risen progressively with each rainy season from 1929 to 1933, resulting in submergence of trees and houses. He also photographed indications of an old beach line approximately 20 meters above the level at that time. Goodrich and Van der Schalie (1937: 8) report similar rising lake levels and mention that 30 or 40 feet above the 1935 level of Petén-Itza quantities of shell of aquatic origin were visible similar to the species then found on the beaches. Shells were similarly observed near Lake Yaxha 13 meters above the 1973 lake level (H.K. Brookes, personal communication).

Such high water levels would have flooded the marginal flatlands in the Peténxil-Quexil area and it is possible that the silty clay soil found immediately south of Lake Quexil dates from this same period, the age of which is as yet unknown.

Nicholas Hellmuth (1973, personal communication) in conducting underwater archeology in Lake Yaxha, reported drowned tree stumps 11 meters under the water, though none were subsequently observed in an afternoon's efforts devoted to obtaining a sample for ¹⁴C analysis.

In the same discussion he reported that the surface of a sacbé believed to have been constructed during Classic times was 3 meters below the lake surface.

The causes of changes in lake levels may be climatic or related to alterations in subterranean drainage. In considering the latter, it is probable that past groundwater levels may be related to sea-level changes. Though subsurface drainage can be exceedingly complex in karst areas, the existence of these lakes in a fault line includes the possibility that such a relation may have been fairly direct. It is also likely that the extreme clay deposition observed in lake sediments dating from the Maya period would have altered this relation by restricting or even blocking the connections between these lakes and groundwater.

Breznik and Fox (1974) conducted a limnological survey of these lakes in the summer of 1969 and described the chemical and biological characteristics observed in their necessarily limited samples. Not surprisingly, they concluded that different criteria than those used to assess the trophic status of temperate lakes are needed to classify tropical lakes.

The lakes which have received the most attention in connection with this project, Lakes Yaxha, Sacnab and Quexil, are remarkably similar. Bathymetrically, all have gently shelving southern shores and deep trenches at the foot of fault scarps on their northern shores. All show CaCO_3 hardness and clinograde O_2 curves. Thermal stratification is regular at all seasons but probably breaks down at night and complete O_2 exhaustion in deep water is rare and temporary.

The phytoplankton community is dominated by Botryococcus though blue-green algae are present. Secchi-disk readings are low (90-140 cm) though productivity is only moderately high. Dark-and-light bottle experiments are limited in number but give a mean of 251.6 ± 121.6 $\text{mgC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in Yaxha (5 experiments), 251.7 ± 110 $\text{mgC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in Sacnab (3 experiments) and 198 $\text{mgC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in Quexil (1 experiment). While these indicate that the lakes are mesotrophic, total phosphorous concentrations in surface waters range from 24 to 44 $\mu\text{g}\cdot\text{l}^{-1}$ in all three lakes (Brenner, 1978) indicative of a moderately eutrophic condition by temperate standards. The disparity between these two assessments may be due in part to attenuation of light penetration caused by the large amounts of inorganic seston observed. Sediment trap samples show that the seston in Yaxha and Sacnab is apparently dominated by re-suspended silt resulting in low loss on ignition (20-40 per cent) while Quexil's seston is mainly dead phytoplankton and forms fresh sediment with 50-60 per cent loss on ignition.

The Zooplankton community is notable for its low diversity and the prevalence of small-sized individuals. Copepods (Diaptomus dorsalis, Mesocyclops inversus, M. edax, Tropocyclops prasinis mexicanis) and the pelagic ostracod Cypria petenensis are numerically dominant throughout the year. Cladocera are scarce with Eubosmina tubicen being the only one of importance. The nature of the zooplankton community is believed to be a response to the presence of at least three planktivorous fishes: the clupeid Dorosoma petenense, the characin Astyanax fasciatus and an unnamed antherinid Melaniris sp. (Deevey, Deevey and Brenner, in press).

Stratigraphic sediment data is relatively incomplete and subject to uncertainties due to diagenesis but indicates that the fossilizing components of the zooplankton (ostracods and cladocera) have been similar and stable in all three lakes throughout the post-Maya period.

Fresh-water molluscs such as Nephronaias, Pomacea and Pachychilas are found in littoral areas and the amounts of their shells associated with Mayan house mounds document a history of exploitation which varied over the period of occupation (Rice, 1976).

Vegetation

The difficulties in description of soils and vegetation have been discussed in the section on soils with emphasis on the relations between the two and the effect of such relations on a soil taxonomy which reflects those dominant factors such as topography and drainage which result in major differences in soil development. It would therefore appear advantageous to describe vegetation in a similar manner.

In this sense, the 'zonal' form of vegetation is broadleaf forest which is mesophytic or quasi-rainforest and although primarily ever-green exhibits a degree of deciduousness proportional to variation in rainfall (Wagner, 1964: 228). The forest is three storied with the tallest consisting of emergents above the closed canopy of the second storey. The lowest storey averages about 10 meters and below this are those herbs, seedlings, shrubs and treelets adapted to the environment created in part by upper storey vegetation. Constituents rarely occur in stands being generally dispersed with variation within the forest

being due to variation in growth characteristics as a response to local conditions rather than variation in composition. Lianas and epiphytes are common.

The major forest association in the area of the Petén lakes is zapotal, the designation being derived from the predominant sapodilla tree Achras zapote. The top storey is composed of Calophyllum, Swietenia, Rheedia, Lucuma, Sideroxylon and Ficus. The middle storey commonly consists of Achras, Vitex, Ficus, Cecropia, Bursera, Spondias, Aspidosperma, Brosimum, Pseudolmedia, Leguminosae and Lauraceae. In the lower storey are Trichilia, Sideroxylon, Sapium, Sebastiania, Miscanteca, Parmentiera, Myriocarpa, Lucuma, Louteridium, Laetia, Dehorsinia, Annona, Sabal, Pimenta, Protium, Ocotea, Zanthoxylon and species of Pithecolobium, Talisia, Cordia and Croton. Such plants as Piper, Psychotria, Ruellia, Justica and palms compose the underwood.

Two distinct variations on this vegetation may be observed, the difference being primarily in the dominants.

Caobal, distinguished by the presence of the mahogany or caoba (Swietenia) is not dominated floristically by Swietenia but consists of forest in which mahogany towers over an otherwise fairly smooth canopy. This form of vegetation has suffered from being selectively logged for Swietenia and Spanish cedar (Cedrela odorata).

The other variation is ramonal marked by an abundance of ramon (Brosimum alicastrum). It is found on steeper slopes and is common on or near archaeological sites. It differs from zapotal mainly in the dominance of the middle storey by ramon though, being found on areas of shallow soil, its canopy is often irregular with frequent large

openings due to blow-downs. Zapotal and caobal are found on the gentle slopes and thus these major divisions correspond to those observed for soils.

Ewel and Myers (1974) have related the forms of vegetation in the Yaxha-Sacnab area to topographical variation and observe what they call "seasonally dry bajo vegetation" located between gentle slopes and the lowland wet bajo. They point out that the change along this topographical gradient is a gradual one but in general the vegetation contains numerous small trees subject to a high incidence of windfall due to the relative instability of the seasonally flooded soil. Trees are short, seldom exceeding 20 meters and the canopy is smooth with palms dominating the understory. These palms are characteristic with Sabal sp. (botanal) and Cryosophila argentea (escobal) respectively increasing in dominance in upland and bajo directions.

Another intermediate form is the corozal described by Lundell (1937: 32). Dominated by the corozo palm, Orbignya cohune with sub-dominants Achras, Swietenia and Ficus, corozals are found along river banks, in valleys and occasionally on hillsides. These areas are those few in which are found the associated deep, moist and fairly drained soils.

Perhaps the most interesting and least understood form of vegetation is that of the bajos. The dominant factors in its distribution and physiognomy are the periodicity and extent of flooding and the drainage characteristics of the soil, such as it is. Conditions are often surprisingly xerophytic due to the extreme moisture deficiency during the dry season arising from the evaporation of surface

water and the unavailability of water in the plastic clay soil. Other areas may be flooded throughout the year at the surface or varying soil depth. Vegetation is generally stunted, small stemmed and dense.

The type form of bajo vegetation is the tinal named for the palo tinta tree Haematoxylon campechianum which often fringes a central pool of water. The height of the tinal varies from 5 to 11 meters with the height increasing away from such a center, though large emergents such as Talisia floresii may be present. While in some areas tinal is composed of shrubs and thickets, the same species will be found in other areas as trees. It would therefore appear that the species present are highly adapted to the general conditions with the local drainage characteristics dominating the physiognomy.

Common trees and shrubs include Haematoxylon, Diospyros, Guettarida, Eugenia, Hyperbaena, Coccoloba, Mimosa, Terminalia, Croton, Caesalpinia, Phyllanthus, Psychotria and Xylosma. The Leguminosae and Euphorbiaceae generally dominate. Lianas are common as are epiphytes particularly Bromeliaceae, ferns and orchids.

A variation on this vegetation is the chechemal dominated by Metropium brownei. These associations of the central bajo intergrade on better drained soils into the palm associations previously described. Herbaceous growth within these associations is scanty and dominated by sedges, though open areas may be overgrown with grasses and various annuals during the dry season.

Within an area of tinal, water may rise to a depth of 1 to 3 meters in the rainy season resulting in the scanty undergrowth. As a result these more easily explored areas have received the most attention in descriptions of bajo vegetation largely to the exclusion of the

denser bajo associations. Lundell describes bajo areas as "uninviting" (1937: 29) as indeed they are but any interpretation of past vegetational changes must consider at least the forces which shape them even if the investigator lacks, as so many others, those personal tastes which might incline him towards their complete exploration.

One may consider bajo areas as a vegetational mosaic whose constituents are composed of highly adapted species with the local physiogonomy under primarily edaphic control. Under these circumstances minor differences in topography and hence soils, flooding and drainage may result in marked differences in vegetation but such topographical differences will also be complicated by variation in rainfall. It may make little difference if in a given year a tinal is flooded by 2 meters of water or 3 yet such a difference can be expected to profoundly alter the edaphic equation in those areas 2-1/2 meters above the tinal affecting in particular the herbaceous vegetation.

While the soil is essentially unstable in the short term where drainage pathways may alter from one year to the next, it may be even more so in the long term if, as is suspected, most of the clay soil is derived from enhanced upland erosion during the period of Mayan occupation. Thus while associations such as tinal and chechemal are present, much of the vegetation in less inundated areas is, and probably was in the past, of a more successional nature as can be seen at present in those open areas seasonally overgrown with grasses. Bank associations may therefore be indicative of other present or past vegetational associations in bajo areas and it is not surprising that many species are common to both.

The transition from forest to river or lake bank is often similar to that between forest and bajo with the same intermediate palm associations being encountered (escobal and botanal) though other areas may be occupied by corozal as described previously. In steeper areas, where such a transition is more rapid, these associations may not be present though a marginal forest of species such as Pachira, Eucida, Ficus and Talisia may occur. At the opposite extreme, low swampy lake and stream banks may be covered with tinal forest.

Gently sloping banks which are seasonally inundated or consist of saturated soil above the high water level support an herbaceous community of grasses, sedges and composites in particular species of Panicum, Spilanthes, Rynchospora, Eleocharis and Scleria though a great many others may occur. If marginal forest does not extend to this zone, a denser herbaceous growth of composites, vines, erect weeds and a few shrub species may be found above it in a highly variable and often diverse association.

With the exception of Talisia, tree species of the marginal forest are rarely observed within bajos, however those grass, sedge and composite species found in the lower bank association are those same species to be found in or at the edges of tinal and overgrowing open bajo areas seasonally. The same sedges though not the grasses or composites for the most part, are found in the swampy grasslands of the central Petén savanna country.

While this is a general pattern for bank associations there are many exceptions, particularly where human disturbance extends to the bank area. Two such exceptions observed on the shores of lakes Yaxha

and Sacnab were a Tradescantia and Scleria association on a low poorly drained bank and an approximately 20 meter wide stand of Mimosa on a moderately sloped bank.

To the south of the string of lakes on the lateritic soils beyond the karst hills described in the section on soils is found mesophytic flatland forest and savanna. While three storied like the quasi-rainforest and often approaching it in luxuriance, the flatland forest is qualitatively different in terms of its constituent species. The dominant species is usually the zacuayum, Matayba oppositifolia associated typically with Zanthoxylum, Ficus spp, Dialium, Caeseria, Bursera, Swietenia, Astronium and Terminalia. Forest composition varies greatly with a lower and more xerophytic forest found on hill slopes exposed to drying winds and more luxuriant forest with increasing numbers of upland forest species found in valleys, swales and around aquadas and seasonal streams.

One of the more important aspects of the flatland forest is that its composition demonstrates which arboreal species in upland forest areas are more adaptable and therefore less informative when observed in the fossil pollen record. In particular, species of Bursera, Zanthoxylum, Spondias and Ficus are found in flatland forest as well as upland forest where they appear to be favoured towards the forest edges. Terminalia and Metropium are found in bajos and flatland forest. Matayba is for the most part restricted to flatland forest.

This adaptability is further shown in observation of the vegetation between the flatland forest and the open savanna. In moving from the flatland forest there is first a transitional belt of xerophytic trees 10 to 20 meters in height. Didymopanax morototoni and Xylopia frutescens

dominate this belt with the former being almost exclusively limited to it. Other common species are Matayba oppositifolia, Spondias mombin, Bursera simaruba, Ficus spp., Alchornea latifolia and Trichilia spp.

This is followed by an intermediate belt of low trees 4 to 10 meters in height which are semi-deciduous. Where fires have penetrated this belt, it is often composed of an almost pure stand of Metropium browneii. Otherwise the characteristic species include Simaruba glauca, Cecropia spp., Miconia argentea, Nectandra sanguinea, Piscidia piscipula, Lippia myriocephala, Zuelania guidonia, Acacia spp., Metropium browneii, Caeseria aculeata, Xylopia frutescens, Bursera simaruba, Curatella americana, Malpighia puniceifolia and Dalbergia glabra.

The outer belt is a fire-resistant thorn-scrub dominated by shrubby melastomes, chiefly Conostegia xalapensis and species of Miconia and Clidemia. Other species such as Vismia ferruginea, Bromelia karatas, and Davilla kunthii are limited almost exclusively to this belt. These are associated with Eugenia capuli and bullhorn species of Acacia.

Scattered fire resistant trees dot the savanna, usually Byrsonima crassifolia and Curatella americana. Others which may be observed include Crescentia cujete, Ternstroemia tepezapote, Dipholis salicifolia, Hippocratea subintegra, Acacia angustissima, Piscidia piscipula and Haematoxylon campechianum. The presence of Haematoxylon, characteristic of tintales, is of interest. The open grassland scarcely exceeds 1 meter in height and is composed of perennial grasses with deeply buried roots, corms and stolons. These regularly burn to the ground during the dry season. A great number of herbaceous species are present, especially sedges and legumes consisting of annuals

passing their vegetative cycle during the rainy season and perennials with underground storage structures.

In addition to the well-drained grasslands, areas of swampy grasslands occasionally occur where soils are waterlogged. These have a characteristic tussock formation of grasses and sedges with very rare to non-existent trees and shrubs.

Lundell (1937: 135) considers the importance of the thorn-scrub belt in its potential role as the major mechanism of reforestation. Invasion of savanna, in his opinion, would involve advance of this and its associated belts as he observed them and would lead to a new successional series on the invaded areas. While this may be the major mechanism for savanna reforestation, it is quite possible that the belts as he described them were a result of an expanding savanna under the impetus of high fire frequency. Lundell describes at length the fires during the 1933 dry season (1937: 92-3) with blazes sweeping not only the grassland and marginal bush, but also entering the mesophytic forest of the flatlands, valleys and hills, burning being observed at nights for two months. Smoke was so thick in the sky that the sun appeared as a red ball and airmail service between Flores and Guatemala City was discontinued for six weeks. This appears to have been an exceptionally dry year with litter in the forest and areas of grassland which had not burned in the three previous wet years being a cause of the extent of destruction. In this respect one may recall Lundell's comment on rising levels of Lake Petén-Itza. The question of savanna reinvasion may depend however, more on climate variability than simply wet or dry periods with the important variable not fire-frequency per year but fire-frequency relative to dispersal and growth characteristics of invading associations or species.

Lundell evidently did not observe Quercus oleoides on the savanna in 1933. Today this species is found towards the edges of the savanna as the central component in islands of apparently expanding arboreal vegetation. While sometimes observed standing alone, it is more often found associated with seedlings and younger trees typical of the intermediate belt described above. Further, it is not surrounded by an outer fire-resistant thorn-scrub belt.

This might imply that at least one component in the reforestation of savanna areas is a decline in fire-frequency such that the survival of the seedlings of species such as Quercus is increased and that such species, being less strongly adapted to fire resistance and perhaps better at seedling growth and seed dispersal are capable of expanding onto savanna areas at a greater rate than species of the thorn-scrub belt and the fire-resistant arboreals when fire-frequency is reduced.

Due to the lack of endemic species, amongst other reasons, Lundell (1937: 94) believes that the savanna represents areas of denuded forest resulting from human disturbance. He states that fire destruction, grazing and man's activity will probably retard any reforestation indefinitely and therefore concludes that the savanna, though at least 500 years old, is a deflected association. The presence of scattered Mayan ruins on or near the savanna would appear to support this argument.

On the other hand, the grassland flora is similar to that found in other areas throughout Central America some of which are known to be extremely old: Wymstra and Van der Hammen (1966) present a 14,000 year record of the Rupununi savanna near Lake Moriru, Guyana.

In analyzing the sediments from Lake Peténxil, immediately adjacent to Lake Quexil, Tsukada (1966) observes maximum presence of savanna at the bottom of his cores from approximately 4000 BP to 1400 BP. This will be discussed later but his general conclusion is that Mayan activities turned a grassland into a high forest rather than the reverse which is common in other parts of the world.

Factors which singly or in combination may cause or determine the existence of tropical savannas include climate, soil, groundwater level, fire, grazing animals and man yet no one factor or combination has as yet been judged able to account for all observations (Beard, 1944, 1953, Bourliere and Hadley, 1970, Budowsky, 1956, Johannessen, 1963). All are possible factors in the Petén and one of the goals of this research is to discern the history of local savanna so that its particular case may be added to the body of data on tropical savannas from which an understanding of them may emerge. While in many cases a particular factor such as hardpan layer or a specific climatic regime may result in savanna, there does not appear to be any such compelling factor in the Petén.

Nye and Greenland (1960: 8) discuss the conditions under which milpa agriculture may cause savanna. Under conditions of increased land pressure, farmers may shorten the fallow period or prolong the cropping period thus reducing the fertility of the soil and the vigour of the forest regrowth when land is abandoned. Grasses and herbs will always invade an abandoned clearing but usually the developing forest species will suppress them rapidly. If the woody regrowth is slow, the herbs form a good cover which may burn during the following dry

season killing the seedlings of the forest trees and resulting in a derived savanna maintained by annual burning. The frequency of fire necessary to sustain such a savanna may be appreciably less on poorly drained soils unfavourable to tree growth while on better drained soils much, if not all, of such savanna would return to forest or closed woodland if protected from fire. Such a successional pattern, in depending on the relative vigour of tree growth, will also be affected by the exact nature of exploitation particularly factors such as the extent of weeding. In most circumstances, a farmer will abandon his plot before declining fertility is a problem, doing so instead when the labour of weeding exceeds the effort required to clear another patch of ground. Even when continuous and efficient weeding takes place up to the time of abandonment, Conklin (1957) points out that the density and topographical location of agricultural plots will be a factor in succession. Constraints on rapid reforestation occur where a site is bordered by or downwind of other swiddens or grasslands which then act as sources of air and animal borne weed and grass seeds.

More recent work has shown that subsequent weed growth is often more a question of viable seed already present in the soil. Kellman (1974) found an average content of 6497 viable weed seeds per square meter of surface soil from 78 sites in pasture and cropped fields in British Honduras. These included 54 species and showed little relation to the weed vegetation, field age, usage or soil conditions. While the full implications are, as a result, somewhat unclear, the observation

includes the possibility that any site which has been previously utilized and allowed to fallow is more likely upon reuse to give rise to a weedy vegetation.

Uhl (1978) studied early successional dynamics after a cut and burn treatment in the forest of the Rio Negro region of southern Venezuela. He found that herbaceous colonizers have their seeds dispersed onto the disturbed site resulting in a time lag in succession during which seed producing individuals develop on the site. Secondary tree colonizers, particularly Cecropia, originate for the most part from seeds or roots in the soil. Establishment of blown-in seeds was observed to depend on features of the microenvironment upon which each seed landed, particularly soil temperature and soil evaporation. Successional dynamics were further affected by the nature and extent of dry season mortality.

In studying vegetational history Uhl's last point deserves some consideration. Since it would appear that differing successional sequences may arise as a consequence of the relative growth rates of herbaceous or woody species immediately upon abandonment, one must consider that climate may play a major role in the outcome. In addition to those parts played by history, treatment, seed availability, soil nutrients and drainage, climatic features such as the distribution of rainfall immediately subsequent to abandonment may result in altered growth rates or mortality. The point may be of limited importance in considering modern agricultural methods but is appreciable when considering vegetational changes and savanna history since the outcome of identical treatment of identical areas might differ according to relatively minor characteristics of the prevailing climate.

Palynological evidence of succession represents the general or average within a basin. Observation of forest succession as indicated by Cecropia and Trema or herbaceous succession, as indicated by Compositae, Cheno-Am and Gramineae, may therefore indicate a general trend in site location, the nature of disturbance, soil alteration, seed availability or climate. In contrast, Ambrosiae is an indicator of active human disturbance, being soon out-competed for light when such disturbance ends. It is observed today bordering well used paths and in the immediate area of dwellings and therefore functions in the cores as in indication of the size of local sedentary populations rather than the nature or result of their activities.

LOCAL MAYAN POPULATIONS

Archeological records of the earliest populations in the area are found in Northern Belize rather than the Petén and demonstrate an Early Preclassic sedentary occupation at the Cuello site from 2500 to 1300 BC called the Swasey phase (Hammond, Pring et al., 1979). Possible indications of human disturbance are found as far back as 4000 BC. Ceramics, architecture and burial practices indicate that the Swasey phase might be ancestral to the Mayan Middle Preclassic (1000-250 BC) in the Petén. Though imported minerals indicate contacts with the Southern Belize and Central Guatemala, comparison of the ceramics with those found at other early sites in Mesoamerica and South America fail to show the source of inspiration or antecedents. Subsistence was based on the cultivation of maize and root crops in addition to hunting and fishing.

In contrast to the distribution thus far observed for Early Preclassic occupation, Middle Preclassic occupation is found not only in Belize but also in the Western Petén at the sites of Seibal and Altar de Sacrificios and it is thought to have taken the form of small villages of agriculturalists exploiting forest and riverine resources. The origin of these populations is the subject of some speculation (Willey, 1975) and while population expansion and migration via river drainages and coastal waters is likely, the possible role of non-sedentary populations, whose presence would be difficult to document archeologically, cannot be discounted.

With the growth and spread of riverine village populations, one may assume that there was a related increase in socio-political organization and intensification of land use. As preferred riverine areas were occupied, groups were forced to move into the interior Petén (Puleston and Puleston, 1971, 1974) establishing settlements such as Tikal where the earliest indications of Middle Preclassic occupation in the central and northeast Petén have been found. Sedentary populations of this period are the earliest observed in the archeological evidence from the Yaxha-Sacnab basin.

Drs. Donald and Prudence Rice of the Florida State Museum surveyed and mapped ten 500 m by 2 km transects radiating north or south from the shores of Lakes Yaxha and Sacnab which represented approximately 25 per cent of the lake basins. Within the total area of the transects, the percentages of topographic, vegetative and soil zones approximated the percentages within the basin as a whole, though bajos were slightly underrepresented. An eleventh survey was conducted on one of the islands of the Postclassic site of Topoxté.

Of the mounds so observed, 23 per cent were sampled by test-pitting and with chronology based on established ceramic sequences, past population growth and settlement patterns for the basin were arrived at by means of assumptions regarding contemporaneity of structures and numbers of inhabitants per structure (Rice 1976, Rice 1978, Rice and Rice in press).

Populations during the early Middle Preclassic occupied widely separated areas on the higher ridges around the lakes, a distribution which may reflect an initial preference for pioneer swidden agriculture in which new fields are regularly cut from primary forest. With

growing sedentary populations, this practice would gradually give way to a cyclic swidden in which a cycle of forest regeneration and recultivation was established. A number of structures from this period appear to be specialized for some ceremonial or civic functions and imply the existence of social differentiation and socio-political authority amongst these early populations.

The preference for high terrain continued through the late Middle Preclassic, though there are areas where residences are found on the slopes, and indications of public architecture increase. Continued occupation of early Middle Preclassic locations appears to have led to the development of at least three distinct socio-political zones including that of the center of Yaxha. Population densities for the basins as a whole reached 24.9 persons/km² by the end of the Middle Preclassic which is equivalent to 1.75 ha. of tall upland forest per person or 2.92 ha. per person if forest of the moist slopes is included. This amount of land is calculated to be more than sufficient to have supported the population even with a need for a 1/3 surplus and 1:6 rotation ratio of cyclic swidden maize agriculture for which the required land is calculated to be 1.92 ha. per person. The utilization of root crops during this period, as indicated by the Cuello data, would more than halve this requirement (Rice, 1978) though, as mentioned in the introduction, the applicability of modern agricultural data to past situations is questionable.

Webster (1975), in an unrelated study, assumes that subsistence was based on the swidden production of maize and has argued that by the end of the Middle Preclassic populations would have become

sufficiently large and dispersed that land shortages might have been felt in the Petén resulting in conflict and socio-political evolution. If early populations were utilizing root crops, it does not seem that conflict would have been a factor in the Yaxha-Sacnab basin though if agricultural mismanagement resulted in degradation of upland forest areas (at present 41.8 per cent of the total basin area) and the use of less ideal areas in terms of labor requirements and yields, some social tension may have resulted. Such a view, however, seems oversimplistic in that it underestimates the flexibility of possible subsistence strategies within a diverse region, not only in terms of fishing, hunting and gathering, but also in the possible existence of a spectrum of agricultural strategies ranging from continuous garden plots to the selective encouragement of desirable species in unfarmed or fallow areas.

In any case, land shortages were probably felt during the Late Preclassic (250 BC - 250 AD) by the end of which population within the basins had reached a density of 60.6 persons/km². Settlement trends observed during the Middle Preclassic continued with increasing density on upland areas and the spread of settlements to the moist slopes particularly in the Yaxha site area. Concentration around three centers of socio-political influence continued though the Yaxha site increased to a greater extent than the other two located on the south shore at the eastern end of Lake Sacnab and on the south shore between the two lakes. Public architecture continued to increase and quantities of obsidian testify to increasing outside trade and influence though the lack of highland products, which are found during this time at Tikal,

may indicate that the Yaxha-Sacnab area was a minor or indirect participant in the growing Mayan trade network.

The limited amount of upland and moist slope forest areas (1.2 ha. per person by the end of this period) would result in agricultural intensification of these and other areas during the Late Preclassic. There may also have been a need for increased surplus production to support larger and more complex socio-political institutions on a regional level as well as greater demands on the individual agriculturalist as the proportion of local non-agricultural population increased. Intensification could have occurred in any number of ways which have the common property of less yield per unit of labor though greater yield per unit of land area. This trend would have continued through later periods with increasing population and socio-political structure though the exact form of intensification at any given time is unknown.

The simplest means of intensification is an increase in the total area of land under swidden cultivation at any one time by decreasing the fallow cycle and utilizing less than ideal areas. Yet to consider only this is to vastly underestimate the flexibility of swidden agriculture as well as that of the Mayan agriculturalist though he may have shared the innate conservatism commonly ascribed to agriculturalists in other places and times. Such a view presupposes a tendency towards monoculture which is so out of keeping with the nature of lowland tropical vegetation that it is difficult to imagine how Mayan agriculturalists ever might have thought of it or why, if a highland inspiration, it was continued.

In keeping with such a supposition, however, models of land use intensification have proposed a change in the staple subsistence base from maize to root crops (Bronson, 1966) or ramon arboriculture (Puleston, 1968) both of which may have offered a greater yield per land area than maize. Doubts have been raised as to the soil suitability, food content and agricultural stability of reliance on either in the Petén. The possibility remains that these crops received increased emphasis particularly in areas where soils, topography, history or settlement density warranted their cultivation rather than maize. The discovery of indications of root crop agriculture amongst early Preclassic populations at Cuello alters the assumption of maize monoculture which was the precondition for the above models.

An alternate or parallel means of land use intensification may have been an increase in the diversity of crops on a single swidden plot either spatially, such as through polyculture, or temporally, such as successive plantings and harvest of a series of different crops prior to abandonment. A continuation of this is possible through exploitation of the fallow stage by planting or encouragement of desirable species upon abandonment or by sparing such species at the time of initial clearing. At its extreme this form of intensification may result in permanent or semi-permanent arboriculture of species such as ramon (Brosimum alicastrum) though again any assumption of monoculture may be misguided.

Intensification may be further achieved by increasingly adapting the strategy of exploitation to those features of soils, topography and history of the specific plot such that the process of land use

intensification may be characterized by an increasing variety of site-specific strategies combining aspects of polyculture, inter-cropping and multi-storied exploitation. Such a pattern of land use has advantages in its resilience to problems of wind, water and crop pests. A further form of variation which affects land use is that of settlement density and it is likely that in some areas exploitation took the form of permanent garden plots with intensive weeding, watering and fertilization. Ultimately land use intensification may have involved major modifications in erosion, water availability, drainage and soil deposition through cooperative projects such as ridged fields. While evidence of these has not been found in the Yaxha-Sacnab area such evidence may be obscured by subsequent clay deposition in the bajo areas where they would have been most effective.

Wilken (1971) discusses the various agricultural techniques available to the Maya and makes the point that subsistence is tied to social and demographic factors rather than simply being a product of necessity and possibility. While means of land use intensification which take advantage of the flexibility of swidden agriculture in such a manner as to evolve site-specific strategies are the most rational course ecologically, the process of intensification which local agriculturalists pursued may not have been constrained solely by the number of options the technology allowed. Patterns of perception, custom and law imposed by the socio-political system of which they were a part, particularly in matters of agricultural specialization, marketing, labor and land ownership, may have been equally important. All that can be said with certainty of the process of land use

intensification which population growth made necessary beginning in the Late Preclassic is that it was successful for the subsequent 650 years.

During the Early Classic (AD 250-550) the social and population trends so far observed in the Yaxha-Sacnab basin continued. (Rice, 1976) While preference for higher terrain was maintained, occupation of sloping areas increased and for the first time residences were located on poorly drained soils. The center of Yaxha emerged as truly dominant in the basins although other centers continued to expand. Social differentiation was more obvious with the construction of large "range" or "palace" structures and complex residential configurations giving the appearance of an increased number of minor centers and a more complex society. This pattern is similar to that at Tikal during this period where continued growth of the major ceremonial complex along with construction of minor centers in the area took place. The social processes this pattern implies are those of increased consolidation and centralization of civic and ceremonial authority, the extension of control through minor centers over an increasingly defined territory and social differentiation involving increasingly limited access to wealth and positions of religious and political authority. Population density in the Yaxha-Sacnab basin had reached a level of 101.8 persons/km² by the end of the Early Classic equivalent to .73 ha. per person of upland and moist slope forest area. The Late Classic period (AD 550-880) was one of maximum population growth with resultant social differentiation and declining land availability. Residences increased in density on uplands, moderate slopes and less well-drained slopes away from the lakes. The most common residential arrangement

was the plazuela usually with one pyramidal structure suggesting the existence of ritual activity at the level of the residence group. Palace structures were added to minor center complexes and residential acropolis areas at the site of Yaxha grew appreciably. These features indicate continuation of the processes of population stratification and centralization of authority. By the end of the Late Classic, population density reached 210.5 persons/km² equivalent to .34 ha. per person of upland and moist slope forest area. From the Middle Pre-classic to the end of the Late Classic population growth in the Yaxha-Sacnab basin was exponential with a growth rate of 0.17 per cent per year.

For unknown reasons, population density during the Terminal Classic (post AD 880) fell precipitously to 21.6 persons/km². Occupation was limited to the immediate vicinity of the site of Yaxha and two minor centers. Settlement at Tikal was also reduced by approximately 90 per cent with residual population scattered in the center itself or in the vicinity of satellite sites. Construction at both Tikal and Yaxha-Sacnab was of small scale and poor quality and activities at Tikal apparently included the looting of tombs, resetting of stone monuments, the burning of incensarios at Classic period temples and the placing of tombs into Classic period construction (Culbert 1973: 74).

An hiatus of unknown duration separates the Terminal Classic from the Postclassic occupation on the islands of Topoxté in Lake Yaxha. While periodic and transient settlement may have occurred and gone undetected, there was apparently no sedentary population inhabiting

the basins during this time. The Postclassic population was distinctly Mayan though differing from local Classic Maya culture in population size, settlement pattern, ceramics, architecture and perhaps socio-political organization.

Some Postclassic ceramic material was recovered from mainland test pits near the Yaxha site which Rice (1976) believes to represent sporadic utilization of Classic period platforms rather than extended occupation. On the islands of Topoxté, Postclassic populations were a highly nucleated community with occupation on the one island investigated consisting of a small civic area on the highest central land surrounded by densely packed residential platforms. The general lack of variation in residential architecture suggests that there was little social differentiation. Population density on the islands is estimated at 11,762 persons/km² with a total population for the Yaxha-Sacnab basins of approximately 5,000 persons.

Since this population was not dispersed it is difficult to compare to previous population figures which were based on observed occupation densities. Further, the area this population may have chosen to exploit may have been greater than the Yaxha-Sacnab basin, a portion of it, or outside the basin on upland areas to the west, and therefore probable exploitive strategies are difficult to assess. Artifact and midden material suggest that snails, turtle, fish, deer and small mammals were major supplements to the diet and further suggest the regeneration of the animal population during the hiatus. The figures for mollusc shells, for example, found in archeological contexts and calculated as shells recovered per occupation period per mound are:

<u>Middle Preclassic</u>	<u>Late Preclassic</u>	<u>Early Classic</u>	<u>Late Classic</u>	<u>Postclassic</u>
24.95	10.7	3.69	2.99	28.26

If one assumes that such a Postclassic population restricts its activities to that area within the 200 m contour used to define the immediate lake basins, the population density within the area would be approximately 125 persons/km², a density equivalent to that during the early stages of the Late Classic period which would require an uncomfortable degree of land use intensification. If one assumes that such a population restricts its agriculture to swidden maize cultivation with a 1/3 surplus and a 1:6 rotation ratio, which requires 1.92 ha. per person according to Sanders (1973: 342-343) and further assumes that it utilizes areas of modern tall upland and moist slope forest, which comprise approximately 70 per cent of the land area, the required sustaining area would be 137 km² or approximately the total area from the lakes out to the nearest putative divide. The actual sustaining area and related degree of land use intensification might have been toward the more confined of these two extremes if that force which caused this population to assume what was an apparently defensive settlement pattern also resulted in a similar nucleation of agricultural areas.

Bullard (1971) found affinities between the Topoxté Postclassic ceramics and architecture and those of Postclassic Mayapan, Yucatan and Quintana Roo. He thought the major occupation dated to AD 1200 - 1400 and that it was abandoned well prior to AD 1618 when Fathers Bartolome de Fuensalida and Juan de Orbita supposedly crossed Lake Yaxha but mentioned no population in the vicinity. In defining the

"Central Petén Postclassic Tradition" which encompassed the lakes of Central Petén and the Upper Belize River system extending westward as far as Seibal, Bullard (1973) attempted to deal with the transitional stages from Terminal Classic to early Postclassic and the limited distribution of Postclassic occupation of which there is less indication either at Tikal and northward or west of Seibal. Data relevant to these points which are fundamental to the full understanding of the Classic Maya 'collapse' are conspicuously lacking.

Within the Postclassic area, he hypothesized that Classic Maya groups survived in some places and that other Mayan groups, moving into the vacuum created by the Classic collapse, combined with the residual groups to create the early Postclassic ceramics and settlements. Such a trend may have continued with intermittent influences from expansionist or migrating groups from the north resulting in the foreign ceramic and architectural features observed in the later Postclassic and perhaps the tendency towards settlement nucleation and island sites.

What little else is known of the Postclassic populations is derived from Spanish chroniclers. In 1525 Cortes reached "Lake Chaltuna" and found the Itza capital of Tayasal said to have existed on five islands. Maler (1910) assigns Tayasal to the islands of Lake Petén-Itza and though Chase (1976) argues that it could have well been Topoxté, it is thought by many to have been on or near the present island city of Flores. The chroniclers also mentioned nine nearby Itza villages including large populations on islands in lakes Zacpui (Sacpuy) and Eckixil (Quexil) and five villages to the east

which were of a tribe at war with the Itza. These included Sacpetén (Salpetén) and Macanché. Upon leaving Lake Petén-Itza, Cortes travelled through open savanna, spending the night at a large lagoon at the end of an eight-league march

The area was subsequently ignored, as far as is known, except for evangelizing efforts by Spanish missionaries in 1618 and 1623. Efforts to reduce the pagan Itza began in 1695 at which time the population was variously estimated at 25,000, 80,000 or not more than 150,000 souls (Means, 1917). These efforts were successful in 1697 when Don Martin de Ursua, governor-elect of Yucatan, took over the Itza capital after a battle upon the lake.

MESOAMERICAN AND SUBTROPICAL PALEOECOLOGY

The study of past Petén environments has been limited not by the efforts applied but by the difficulties of obtaining sedimentary material of sufficient age and fossil content. While the latter is largely the result of the profound effects of past human disturbance, the reasons for the former are less clear. In many cases, experience has shown that the perverse nature of montmorillonite clay sediments challenges the stamina of portable coring equipment and its operators; yet even with luck and perseverance, the age of the sediments which may be penetrated has been at best mid-Holocene. This may be a result of the youth of the lakes, the deposition of a layer of impenetrable sediment at that time, or a temporary decline in water level; yet resolution of the question demands longer records.

The most complete paleoecological study is that of Lake Petén-xil adjacent to Lake Quexil (Cowgill et al., 1966). Cores were obtained in four meters of water and document the results of local Mayan disturbance through analysis of chemistry, pollen, plant microfossils, diatoms, sponge spicules and animal microfossils. The depth of sediment penetrated was 260 cm in core 2 and 225 cm in core 3 with ^{14}C ages of approximately 4,000 and 2,200 years BP respectively. A 54 cm section of core 2 was reportedly disturbed on extrusion and used as a ^{14}C sample giving an age of 2,880 ^{14}C years BP.

This results in a situation where core 3 in its entirety agrees closely with core 2 above the lost section and there is a regrettable discontinuity in the record from about 2,200 to 3,500 ^{14}C years BP. ^{14}C dates are uncorrected for atmospheric ^{14}C variation and, more importantly in this karst area, for carbonate error (Deevey and Stuiver, 1964) making interpretation of the cores questionable when related to the established Mayan chronology.

Evidence for human disturbance in the area exists throughout the length of these cores, though there are great variations in its extent suggesting marked oscillations in the local population. The authors find no indications of significant climatic change, disastrous increases in erosion rates or serious population pressure.

During the earliest period (G 1) before 3000 BP, vegetation was dominated by savanna with a small percentage of arboreal pollen dominated by Moraceae and Quercus. The presence of agricultural man is demonstrated by pollen identified as Zea (Tsukada and Rowley, 1964) and a high incidence of charred grass fragments attributed to clearing by fire. High frequencies of Botryococcus and Pediastrum with low sponge spicules and Cladocera indicate that the lacustrine environment was quite different from today's. Total and exchangeable potassium, sodium, calcium and the grass fragments are interpreted as indicating an episode of agricultural activity around 3900 BP involving the utilization of savanna.

During the middle period (G 2) from 3000 BP to about 1200 BP Moraceae and Terminalia decline, Quercus and composites increase and grasses continue to be abundant. Zea reaches its maximum at about 1600 BP and charred grass fragments, though present, are at a very low

level relative to the abundance observed in G 1. The planktonic population shifts in favour of the Cladocera and changes in the ratio of littoral to planktonic-Cladocera suggest a lower lake level in G 1 and in the later half of G 2 with a higher level during the intervening time. Three major episodes of agricultural activity are observed during this period: in the first century BC, around the fifth century AD and about 900 AD.

During the late period (G 3) from 1300 BP to present, grasses and composites were reduced while Moraceae and Terminalia increase. A very small rise in Zea at 600 BP with which the chemistry is relatively concordant is interpreted as the last agricultural episode. Subsequently there was a period of intense erosion and deposition which it is suggested might result from an earthquake and up-lifting of the southern shore.

Details of this interpretation are questionable, as previously mentioned, due to the dating control yet clearly the periods of human activity involved a marked reduction of forest and a much greater proportion of savanna and Quercus than observed today. Grasses and Quercus form a large proportion of the pollen in the G 1 period when composites are very low and maintain this level during the G 2 period when composites are high. At the G 2 - G 3 boundaries all three decline and reforestation evidently takes place. This led Tsukada (1966) to conclude that Mayan activities had in some manner caused savanna to be turned into a high forest. While climatic change is categorically denied, observations on lake level changes which may be climatic are not related to vegetational changes and the behaviour of the carbonized

grass fragments is left unexplained. Pollen data is presented as percentage of total tree pollen with the result that, lacking an influx diagram, the proportions of change may be misleading. Reliance on uncorrected ^{14}C dates makes it necessary to interpret a slight rise in Zea, grasses, composites and Quercus at a single level as representing the local Postclassic. If Tayasal was in fact at or near Flores some 5 km to the west, and there was, as reported, an Itza village beside Lake Quexil, this appears an inadequate degree of disturbance. This and other points of the interpretation would benefit from archeological study of the area.

Tsukada and Deevey (1967) used the zonation established for Lake Peténxil in studying cores from Lake Izabel and three highland lakes but their oldest sediments (in Lake Amatitlan) are probably no older than 1000 BC. Most if not all changes observed are believed to be due to human disturbance which, while most prominent during the Classic Maya time, did not diminish during Postclassic and Postcolonial times to the same extent as in the Petén.

Increases in the abundance of molluscan shells in a 3.7 meter core obtained in Lake Petén-Itza near Flores were interpreted by Covich (1976) to indicate either slumping of sediment from the littoral zone or brief periods of lowered lake level. Shell zones were located at 0.4 meters and between 3 and 3.7 meters but the core was not dated. Stratigraphically similar shell zones were observed in Lake Salpetén sediments.

Covich and Stuiver (1974) interpreted changes in molluscan abundances, 180:160 ratios, sedimentary laminae and exchangeable calcium

concentration in a 12 meter core from Lake Chichancanab in central Yucatan as indicative of past lake level fluctuations. The core was obtained in 1.5 meters of water since at deeper water sites (8 and 12 meters) samples could not be obtained below 3 meters of sediment depth due to the hard crystalline nature of the sediments. The lake began to refill after a long period of reduced volume or complete dryness about 8,000 years ago. During the subsequent 2,500 years the lake is thought to have remained shallow with a productive littoral zone near the coring site. There are indications in the data, however, that suggest a progressive decline in lake levels from an initial high stand. Lake level is thought to have increased 5,500 years ago and then to have remained stable for 4,000 years, declining to its present level 1,500 years ago. These dates are based on non-woody organic material and may therefore be overestimates due to carbonate error. The 8000 BP date is based on carbonate marl corrected for a measured ^{14}C deficiency in modern carbonates.

Lake filling about 8,000 years ago is also observed in Florida at Mud Lake and Lake Louise (Watts, 1969, 1971) and is interpreted as being due to the effect of rising sea level on water tables. Similarly, at Little Salt Spring, a sinkhole in southwest Florida, water level rose from -26 m to within 1 m of its present level during the period 12,000 to 8,500 uncorrected ^{14}C years BP (Clausen, Cohen, Emiliani, Holman, and Stipp, 1979). By 5,500 ^{14}C years BP water level had dropped 8 m and subsequently rose to its present level. Paleobotanical evidence indicates periods of wetness between 9,000 and 8,000 years ago and again during the last 4,500 years. Pollen from Lake Louise and Mud Lake support this

pattern in indicating dry forest or oak scrub between 8,500 and 5,000 ^{14}C years BP with subsequent mesic forest existing to the present.

To the south of the Petén, Bartlett and Barghoorn (1973) interpret a similar climatic sequence for the Gatun Lake basin of Panama. Their study is based on sections from a number of cores drilled by the Panama Canal Company and its most successful aspect is the development of a curve for sea-level rise based on Rhizophora pollen. Climatic interpretation is somewhat constrained by the limited number of levels counted, the fact that only 200 grains were counted at each level despite a remarkably diverse pollen rain and the resultant difficulty in establishing zonal boundaries or general trends. It appears, however, that by about 8,000 to 8,500 ^{14}C years BP vegetation was similar to today's after a previous cooler and perhaps wetter period. Between 8,000 and 4,200 ^{14}C years BP, the presence of Myrica and Ilex, which reach maxima at about 5,000 ^{14}C BP, suggest a climate that was drier and more seasonal than at present, based on their present distribution in Panama. From 4,200 ^{14}C years BP to the present, fresh water swamp vegetation was well developed and there was no evidence of the possible dryness of the previous period. During this period Gramineae, Cyperaceae, Compositae and Zea increased as tree pollen concurrently decreased suggesting that human disturbance was the major cause of observed vegetational changes.

Wymstra and Van der Hammen (1966) present a complex history of the tropical savannas in Colombia and Guyana suggesting an unstable equilibrium between open savanna and dry forest or savanna woodland which is affected by climatic changes or human disturbance. In the Llanos Orientales of Colombia, open savanna areas appeared around 3000 BP,

perhaps as a consequence of human disturbance, and have persisted to the present. An earlier period of open savanna between 5000 and 4000 BP suggests a drier period at that time and there are indications of seasonal drying up of the lake. Woodland savanna is present to the bottom of the core at about 5200 BP. In the Rupununi savannas of Guyana there were repeated changes in the proportions of open savanna and savanna woodland between about 9000 and 5000 BP. From 5000 BP on, and especially in the last 3,000 years, open savanna has dominated.

Van der Hammen has produced a number of studies from the highland areas of Colombia, though their relevance to the Petén may be questioned on the basis of altitude and latitude. Suffice it to say that he is able to demonstrate late-glacial and post-glacial pollen zones in this area which are perfectly synchronous with European phases.

It is obvious that data on Holocene climates is rather sparse through Mesoamerica and any pattern discerned along this latitudinal gradient must be very tentative as a result. The conceptual basis for such pattern may be that past climatic changes should be synchronous or that they should relate to some model of the process of climatic change in which case the manner in which change differs along such a gradient in quality and timing is the important aspect. The questionable accuracy of ^{14}C dates subject to varying degrees of carbonate error throughout this area presents the greatest difficulty to the resolution of past climatic changes. Other difficulties have as their basis the nature of the climate which, in being highly seasonal, makes general descriptions such as "wet" or "dry" fairly meaningless. For example, an observed "dry" period based on vegetation may indicate decreased total rainfall,

an increased seasonality (wetter wet season and drier dry season and/or shorter and longer respectively), an increased yearly variability (wetter wet years and drier dry years and/or fewer and more respectively) or any combination of these. Precise knowledge of what exactly observed "wet" or "dry" periods mean must form the basis for any understanding of the process of climatic change.

One may also note that an observation of dryness may depend not only on the form of dryness but also on the degree of that particular form at which it will be expressed by that being observed. In other words, given a type of dryness, tropical forest will have a threshold for that type beyond which that dryness will be expressed by vegetative changes but that threshold will be different for savanna, for plankton, for human social systems or for sediment chemistry.

Comparison between histories of lake levels in Florida and Meso-america is complicated by their ability to be affected by sea-level changes acting on the groundwater level. The physical complexity of the Caribbean and Gulf of Mexico also make it likely that rising sea-level would cause changing oceanic current and surface temperature patterns. These might result in climatic alterations which are local rather than a reflection of change in the global system.

In view of all this, the apparent similarities as well as differences between the climatic records for Florida, Panama and the South American savannas emphasize the need for a more complete record for the Yucatan-Guatemala lowland area in order to clarify their meaning.

Paleoclimatic data from tropical Africa is far more abundant though sequences conflict more often than not and result in a degree of confusion. Some of this confusion may arise from those difficulties discussed

above but much appears to be due to the complex climatic pattern of Africa (Flint, 1971). Though climates are seasonal, seasons throughout the continent do not coincide due to distortion of the symmetry of the broad atmospheric circulation pattern and hence the seasonal system of winds and precipitation. Greater heating of the land than the sea surface leads to areas of low pressure over tropical Africa and in summer over Asia resulting in pressure troughs whose strength and position shift seasonally distorting the shape of the tropical and subtropical belts of low and high pressure. Such distortion, most easily viewed as bending of the Inter-Tropical Convergence, also takes place in tropical South America and the southwestern United States. For example, in comparing the records from Panama and the tropical savannas, it must be remembered that though at similar latitudes, a southward loop in the ITC during January over South America makes the savannas further from the low pressure belt than Panama at this season and thus more likely to suffer lower first quarter rainfall if the general strength of circulation increases. One of the major attractions of the Yucatan-Guatemala area for paleoclimatic studies is that the ITC is not locally distorted by land masses and its climatic history may therefore be highly indicative of global patterns.

For Africa, as Central America and elsewhere, inter-regional comparisons of climatic records show both similarities and deviations which may serve as a basis for creative paleoclimatology yet the climatic complexity of Africa makes it impossible to suppose that any single climatic record may be of relevance to Mesoamerica. The sophistication of Pan-African climatostratigraphic paradigms continues to evolve but

such paradigms are too often rigid and simplistic and suppress regional contrasts and anomalies (Butzer, Stuckenrath, Bruzewicz and Helgren, 1978). In view of this, it may be that the most fruitful strategy will be to produce climatic reconstructions of particular periods with the supposition that any single observation should be considered as a statistic that defies full interpretation unless considered with other members of the statistical ensemble. Webster and Streten's (1978) reconstruction of the glacial-age climate of tropical Australasia and the inferences they are able to draw in consequence is an excellent example of this. Such a strategy does little, however, for the present purpose of attempting to discern which past climatic features in the African records might have had equivalence in the Petén. Any such features must be looked for in those attempts at synthesis and paradigm construction whatever their inadequacies.

Pollen analysis and the interpretation of vegetational change in tropical areas present great difficulties, some of which have already been mentioned. The result is that generalities about past climatic changes in Africa have been more confidently inferred from past lake level fluctuations and dune formation, which, while less able to give insight into climatic subtleties, are readily comparable. The equatorial lakes of the East African plateau show an early Holocene high stand between 10000 and 8000 BP with increasing levels beginning about 12000 BP prior to which lakes were much smaller. After 8000 BP there was a decline in levels but the subsequent record is more complex with great variation between lakes even within this limited area. An apparently concordant increase in lake levels occurred between 6000

and 4000 BP but aside from this each lake shows a unique history of fluctuation between low and moderate levels relative to which modern levels are low. It is suggested that high lake levels were associated with increased precipitation rather than reduced evaporation (Butzer, Isaac, Richardson and Washburn-Kamau, 1972).

Some lakes in this area such as Lake Naivasha (Richardson and Richardson, 1972) show a history which is more in common with the climatic sequence of the southern Sahara. Lake Naivasha was at a high level between 9200 and 5650 BP, shrinking between 5650 and 3040 BP until it dried up briefly. Since 3000 BP the lake has been small, though frequently being smaller. Evidence from sand dunes and marl beds of former lakes in the southern Sahara suggest a moist climate prior to 30000 BP, a dry climate until 12000 BP and then a wet climate from 12000 to 3000 BP with a transitory phase between 5000 and 7000 BP (Livingstone, 1975). There are indications that conditions were somewhat drier than today around 3000 BP.

Sarnthein (1978) in reviewing a vast amount of literature of dune formation and lake levels in the tropics and subtropics finds periods of humidity between 10000 and 7500 years BP and between 6500 and 5000 years BP, the latter in partial contrast to Livingstone's (1975) synthesis

It is difficult to overstate how inconsistent much of the evidence is, perhaps due to local differences in the relative extent of changes in precipitation and evaporation at any given period. The continued emphasis on recognition of synchronous wet and dry periods as expressed by lake levels and dune formation may only be productive in arriving at

coarse similarities. In essence, there are distinct levels of generalities. The presence of an early Holocene moist period is quite universal in tropical Africa as are relatively dry modern conditions. A moist period around 6000 BP following a dry period and a dry period around 3000 BP are common though not universal. Beyond this, observed climatic phases appear to be largely local phenomena occurring as a net result of changes in temperature, evaporation and precipitation under the local seasonal regime. Resolution of the climato-stratigraphic sequence in Africa may depend upon discoveries in other tropical areas which are not marked by such a complex climatic pattern.

The situation is similar for tropical Australasia where beyond a general sequence similar to that observed for Africa, climatic sequences vary locally, probably due to the complex climatic pattern resulting from the configuration of land masses and ocean currents (Bowler, Hope, Jennings, Singh and Walker, 1976).

A sequence which is relatively free of such constraints is that observed by Colinvaux (1972) for a crater lake in the Galapagos islands. Located on the equator and within the Central Pacific Dry Zone caused by reduced circulation due to cool surface water, the direct relevance of this sequence to the Petén is questionable. Colinvaux's analysis demonstrates an ephemeral lake from 10300 to 8600 BP following a dry crater, altering to a permanent pond between 8600 and 8000 BP. A larger lake existed from 8000 to 6200 BP and a fluctuating shallow lake from 6200 to 3000 BP. From 3000 BP to the present there has existed a deep lake. This sequence conflicts with Sarnthein's (1978) generalities.

The effects of past human and climatic disturbance on the local environment are difficult to differentiate and it would be desirable to have an established climatic sequence with which the record from the Petén lakes area could be compared as an aid in interpretation. Though it is clear that climate has varied significantly over Holocene time in the tropics, the number and diversity of sequences observed make it impossible to assume that any one sequence or any generalities derived from a group of sequences will have parallels in the Petén records.

CONSIDERATIONS FOR TROPICAL PALYNOLOGY

In any part of the world, palynology attempts to infer from the changing amounts of pollen which have settled on a small area of lake bottom the changes in vegetation of which they are a product. Though properly a tool of paleoecology, palynology is sufficiently complex to be often considered a specialized discipline. The practice of palynology in tropical areas presents difficulties which are not in fact unique but rather are extensions of difficulties which already exist in temperate palynology. It is not the object here to review in detail all the difficulties of temperate palynology, and it must be presumed that the reader already has a familiarity with many of the problems presented by differences between species in pollen production, physical constraints on dispersal in air, differential settling rates in water, sediment focussing, sediment mixing, differential preservation, sampling, processing, microscopy, pollen recognition, calculations, differentiation between local and regional representation, and so on. In these aspects tropical palynology varies little from that practiced in temperate areas. The major causes for special concern are the limited representation of the total vegetation and the processes of vegetational change.

To a much greater extent than in temperate areas, the "universe of 100 per cent" represented in pollen diagrams is not even approximately equivalent to the total vegetation in the area. It is equivalent

at best only to the universe of the pollen rain and the relation between the pollen rain and the total vegetation in terms of representivity may be expected to vary with vegetational changes. This relation will reflect as an initial approximation, the extent to which vegetation is composed of anemophilous species, a feature which will vary over time. In practical terms, then, an observation such as the high proportions of Moraceae in the lower sections of the Quexil core will be a representation of at least two features: relative expansion of forest and/or relative dominance of Moraceae within existing forests. There is no firm basis on pollen evidence alone for estimating the relative dominance of these factors in producing the observation.

With respect to vegetational process, it must be kept in mind that there is no reason to presume that present-day vegetational associations are persistent over time. Livingstone in particular has emphasized that tropical species subject to a changing environment react as individual species and that the result is not an altering of the relative proportions of deterministic vegetational associations but rather changes in the types of associations present. While this may be less true for stressed vegetation types such as savanna, the result is that interpretation of vegetational changes as expressed by pollen must depend on the observed characteristics of species and not associations. In theory, at least, it is possible for an environmental parameter to be such that no present day vegetational association is present yet the pollen spectrum observed may be identical to today's.

These considerations lead to the result that pollen alone is inadequate for confident interpretation of historical processes in tropical areas and that any paleoecological hypothesis must have as its basis consistency with as many forms of stratigraphic evidence as are available. One such form of stratigraphic evidence is analysis of the carbonized plant fragments in the sediments.

Carbonized plant fragments in sediments and the information they contain have been largely ignored in the past. Exceptions are Waddington (1969) and Swain (1973) working in Minnesota, Tsukada and Deevey (1967) in Central America and Green (1976) in Nova Scotia. What is mainly lacking is a conceptual model to account for the observed changes in the numbers and types of fragments observed. As with pollen, the set of assumptions to explain a sample at any one level are often so complex as to render rigorous interpretation questionable but these tend to cancel out when the desired end is to account for changes occurring through a stratigraphic sequence. It has been the intention of previous authors to see whether a correlation exists between carbonized fragments and vegetational changes and, with the exception of Tsukada and Deevey, the measure of fragment content has been total surface area per cm^2 per year.

As Swain (1973) points out, fire on surrounding slopes will lead to increased erosion as well as increased nutrient input to the lake. Both these factors combine to render such a measure questionable to the extent that fire intensity could not be expected to be proportional to the height of a charcoal peak. Further, fire would be an isolated event whose effects would be diluted by sediment mixing. In an attempt to correct for these effects, Swain uses a fragment: pollen ratio thus

eliminating false charcoal peaks due to isolated events of sediment redeposition and the reverse due to dilution, though such correction cannot be perfect since a large fire should result in an immediate change in pollen input due to tree mortality and/or high pollen producing successional species. Green (1976) follows these methods with the addition of some complex statistical analysis. In all cases information contained in the size spectrum or types of carbonized fragments observed has been largely ignored. This is an admissible and perhaps necessary oversight given that one is dealing with the burning of woody species but forms the main source of information in dealing with grassland fires.

A forest fire would yield a rather mixed spectrum of fragment sizes at source according to fire intensity, extent of desiccation and type of vegetation. It could be expected, for example, that herbaceous tissue would yield a greater proportion of larger types than woody tissue and thus an observed increase in the proportion of large particles at source could indicate increased ground cover, thicker ground debris, extent of desiccation of leaf tissue or, conversely, a decreased amount of burning woody tissue, i.e., the situation is exceedingly complex. To sort out from this the effect of decreasing proportion of larger types at increased distance of source is thus unfeasible in the case of forest fires: distance is simple one of a number of variables affecting the size spectrum observed in the sediments.

Initial observation in the Quexil sediments, however, revealed as in Peténxil, a preponderance of grass tissue represented as carbonised fragments and the assumption that the major source of these

fragments is burning grassland areas simplifies the situation: 1) the types of tissues burning and their physical location within a vegetational structure as variables are sharply reduced; 2) given this, the extent of desiccation of varying tissue types and the subsequent effects on what will or will not burn within the vegetational structure is also reduced; 3) the variability introduced by fire intensity is reduced: as a generality, one is forced to presume that a grassland simply will or will not burn. As a consequence of these assumptions the effect of distance on the size spectrum of carbonized fragments within the sediments becomes a less attenuated variable though it should be emphasized that this model is not applicable to carbonized fragments from a forest area where no grasses are present.

Given this model, one may make the assumption that the proportion of larger fragments should decrease with increasing source distance as a function of transport phenomena. Direction of source in relation to prevailing wind patterns will also affect the size spectrum. This relation should hold true whether fragments are blown in or washed in, the latter being less of a problem given the high rate of degradation of fine organic matter on the soil surface in tropical areas and the probability of fires occurring during the dry season. While the resultant extent to which one may interpret a particular sample is highly questionable, interpretation of changes within a stratigraphic sequence should be valid.

METHODS

The Lake Quexil core was obtained in 1972 by the author and Dr. G.H. Yezdani at the deepest point of the southwestern basin of the lake in 7.2 meters of water using a 1-1/2" Livingstone corer. Total length of the core is 6.4 meters bottoming in an impenetrable layer of apparently sub-baked clay with limestone fragments. Under conditions of lower water level, this basin may have been separated from the deepest portion of the lake.

The Lake Sacnab core was obtained in 1974 by the author and Dr. D. Rice towards the central part of the southern shore of the lake in 7.5 meters of water with the same corer. Lack of casing necessitated an excessive amount of hammering and resultant failure of the coring equipment prevented bedrock being reached. Length of the core is 6.3 meters and there is reason to believe an additional .75 meters of sediment remained unsampled.

Both cores were transported to the Florida State Museum where they were extruded, described and sampled for loss on ignition, pollen, aquatic fossils, carbonized fragments and ^{14}C dates. Subsamples of .5 cc were processed for pollen by standardized methods of deflocculation with 10 per cent KOH, removal of carbonates with 10 per cent HCl, removal of silicates with HF, followed by acetolysis and mounting in glycerol. No oxidation or staining was done. The HF method utilized was immersion in cold mixture of one part 40 per cent HF and five

parts 10 per cent HCl for 24-30 hours. Throughout the procedures of extrusion, subsampling, chemical processing and mounting, pollen traps were left in the area and subsequently checked for possible contamination. Only one $28\ \mu$ graminoid grain was ever found, the windows of the laboratory being permanently sealed and filters placed over the air-conditioning and fume-hood inlets.

Pollen samples from the Sacnab core were processed by M. Brenner of the Florida State Museum. Chemical analyses referred to in this study were performed by S. Flannery of the same museum. Pollen and spore identifications were based on the pollen collections of E.S. Deevey and published material principally that of Tsukada (1963, 1964a, 1964b) and Bartlett and Barghoorn (1973).

Initial analyses of the Quexil core were performed in 1973 by the author and Dr. G.H. Yezdani, the results of which are included in the appendix of this dissertation. Pollen was counted under $300\times$ magnification and standard light conditions. For the other fossils, .19 cc sediment samples were deflocculated and mounted in Canada Balsam. All fossils were counted over a measured fraction of each slide.

It may be noted in the prior section on vegetation that there are a number of arboreal species which may be characterized by their adaptability, being found in savanna edges, high forest, bajo areas and points between. Distressingly, these same species are those which also produce large, easily recognizable pollen. The result is that, using counting techniques, particularly as regards magnification, based on temperate zone practice, information obtained tends to a) overemphasize stressed areas such as savanna or early successional stages where

a major proportion of species are anemophilous, and b) lead to minimal information regarding vegetational changes in forested areas.

Those species which are more specific in their present distribution tend to have excessively small pollen and thus insights into forest disturbance depends on careful pollen counts under high power. Analyses for this study were performed under phase-contrast at 750 x magnification.

Because of the diversity of pollen observed, emphasis was placed on achieving high pollen counts where possible, despite the advantages for statistical analysis of counting only 200 grains per level. For Quexil the mean pollen sum, which excludes exotics and aquatics, is 812 grains. The Sacnab core contains large sections where pollen is rare and badly preserved resulting in a mean pollen sum of only 541 grains. In the resulting pollen diagrams all pollen are expressed as a percentage of the pollen sum. While counting the pollen slides other fossils such as various types of spores, turbellarian egg capsules, carbonized fragments, Botryococcus and Pediastrum were also counted.

Samples of .455 cc of wet sediment to which a known amount of Lycopodium pollen had been added were treated with 10 per cent KOH, 10 per cent HCl and mounted in glycerol. These were used to count the carbonized fragments and to convert the original pollen figures into measurements of pollen density (grains/cc).

Carbonized fragments were noted in a matrix of seven size categories (less than 200 μ^2 , 200-500 μ^2 , 500-1000 μ^2 , 1000-2500 μ^2 , 2500-5000 μ^2 , 5000-7500 μ^2 , 7500-10000 μ^2 or individually measured)

and three type categories the latter being: 1) Gramineae, 2) probably Gramineae but without sufficient surface features for certainty 3) unknown, dicot and woody. The latter category was dominated by small fragments which would include fragments derived from wood tissue. The occurrence of definite dicot or large woody fragments was exceedingly rare. No differentiation as to type was attempted on particles smaller than $200\ \mu^2$. Total surface areas for each category were calculated by multiplying the number of fragments by the arithmetic mid-point of area of that category.

The reasoning behind the use of surface areas rather than the number of fragments in previous studies is obscure and, from previous discussion, possibly misleading but it is used here quite purposely to compensate for characteristics of the data. Any grass fire at source will produce a spectrum of particles and the point in attempting to discern distance of source is the presence of larger particles. While simple number of large particles might suffice to do so, the relation is more clearly brought out by use of surface areas represented by each size category thus emphasizing the presence of the larger fraction in direct proportion to their size, i.e., the use of surface area compensates for the fact that while a distant fire will be represented mainly by smaller fragments, a lakeside fire will, in addition to being represented by large particles, also add to the smaller particle category. A similar situation exists with types where the use of surface areas attempts to compensate for the relation between size and the ability to differentiate as to type. In both cases, the use of numbers alone within each category would result in an underexpression of the desired information.

Note that if fragments do not derive from grassland fires, one might be misled to a degree by the type analysis due to the simple probability that any grasses within or near the burning vegetation would generate larger size particles and the emphasis due to the use of surface areas may cause the spectrum to appear to be derived from grass land. On the brighter side, the presence of such fragments under such conditions forms a basis for the size versus distant relation which otherwise would be invalid, i.e., where Gramineae particles are not present, variation at source must be assumed to dominate the reasons for the size spectrum.

The addition of Lycopodium pollen allows for the derivation of carbonized fragment density (μ^2/cc) in the standard manner (See Appendix). While counting the carbonized fragments, other elements were also counted including pollen of Pinus, Podocarpus, Gramineae, Compositae, Quercus plus Quercoid, turbellarian egg capsules, the larger spores, Botryococcus and Pediastrum. The smaller of these were treated with less confidence according to the extent to which they were obscured due to sediment type. Comparison between these counts and those for the pollen allowed for a number of independent conversion factors at any given level the mean of which was used for converting the original pollen sum to pollen/cc (See Appendix). At the 4.5 meter and 5.2 meter levels the scatter of these factors was judged too great and the final pollen/cc value used for subsequent influx calculations is in each case the mean of the two values from the levels above and below it. The results of these methods were calculated as total carbonised fragments per cc, pollen/cc and the size and type categories as percentage of the total surface area. Sedimentation rates and influx calculations will be considered in a later section.

RESULTS

All lakes observed in this area contain, in their sediments, a layer of silty clay the thickness of which appears to be related to the extent of local Mayan disturbance as a first approximation. The sediment stratigraphy of the Lake Sacnab core (Figure 4) shows such a clay layer clearly with layers of gyttja above and below it. Lenses of increased clay content occur in the lower gyttja layer while lenses of increased gyttja content occur towards the bottom of the clay layer. Percentage water content and percentage loss on ignition curves clearly reflect this physical stratigraphy.

The physical stratigraphy of the Quexil core is more complex (Figure 8). Bottom sediments suggest bajo-like soil with initial filling of the lake associated with a high content of coarse plant material. Among this plant material was a large wood fragment used for a carbonate-error free ^{14}C date. Subsequent alterations between coarse and fine gyttja may be indicative of shallow and deep water conditions, the coarseness being due to proximity to the littoral zone. Equally, coarse gyttja may be due to movement of sediment from a littoral zone to the coring site under conditions of fluctuating lake levels.

From 350 to 230 cm there is an increasing content of coarse plant material as well as a single shell layer at 340 cm. At 230 cm sediment changes to gyttja and then clay-gyttja at 205 cm and gyttja at 85 cm.

Shell layers occur in the area of the changes in sediment type. Between 135 cm and 143 cm finely laminated sediments occur of lower clay content.

The original results of the percentage water and percentage loss on ignition analyses were later found to have been incorrect due to the tendency of the clay to retain water even after 24 hours in a drying oven. This resulted in an underestimation of water content and an overestimation of loss on ignition for the clay layers as well as a disturbing tendency for the samples to occasionally explode in the muffle furnace. Figures presented here are the results of later analysis by S. Flannery of the Florida State Museum for total C, total N and total P. Of the total C, later analysis showed that CaCO_3 carbon is especially significant between 110 and 170 cm where it averages approximately 50 mg/gm of dry sediment, values ranging from 3 to 8 mg/gm below this section and 7 to 14 mg/gm between 35 and 100 cm. Values averaging approximately 50 mg/gm are found above the 30 cm level. Thus while it would appear from the curves for total C and total N that both vary clearly with sediment type with a consistent C/N ratio, in reality the organic C/N ratio is higher in the lower levels averaging 16.5 below 230 cm. This suggests the presence of organic matter of littoral, bog, or allochthonous origin. The laminated sediments at 135-145 cm also have a high C/N ratio of 21.08 at 145 cm and 16.8 at 135 cm. Other sections of the core above 230 cm vary between 12.5 and 14.5 with the section above 30 cm having lower values of around 10.

Deevey, Rice, Brenner and Flannery (1978) show that the total P, when calculated as influx to sediments, is proportional to the intensity

of human disturbance for Lakes Yaxha and Sacnab. The total P in the Quexil sediments is probably related to disturbance in a similar manner though the lack of archaeological data for the basin restrains certainty. If so, the decline in total P between 420 cm and 480 cm may be a result of altered sedimentation rates or a change in the location of limited human disturbance at that time.

The initial pollen analysis (Figures 11 and 12 in the appendix) could be related to the Peténxil results and showed that the Quexil core penetrated sediments of greater age. On the basis of the curves for Moraceae, Ambrosiae, Compositae and Gramineae, the equivalent in Quexil of the bottom of the Peténxil core is approximately 270 cm. It may be observed that before this period of grassland, high forest had existed and was perhaps more widespread than today. Other features of interest are the succession of aquatics at the time of initial lake filling and the indications of human disturbance (Ambrosiae, Compositae, possibly Cecropia) as far down as the 530 cm level.

If one assumes that all observed changes are due to human disturbance, then this pollen analysis suggests that Mayan populations acted in such a manner as to remove forest and promote grassland until the time of local abandonment, indicated by the sharp decline in Ambrosiae and Compositae at 70 cm. Following abandonment, reforestation took place as suggested by declining Gramineae and increasing Moraceae. There is little in the other pollen curves which cannot be interpreted in a manner consistent with such a scenario. Comparison of this record with that of the aquatic fossils, however, introduces greater complexity.

The abundance curve for Ostracods, Gastropods and Bosmina in particular (Figures 14 and 15 in the appendix) shows that the 2 - 3 meter section of Moraceae decline and increased grassland was also one of transition in the lake itself. This is further demonstrated by the changes in the physical nature of the sediment from coarse gyttja with macrofossils to gyttja with shell layers and a lower C/N ratio. The changes in the abundance of plant tissues, fungal spores and carbonized fragments (Figures 13 and 16 in the appendix) the latter also observed in Lake Peténxil, suggest that the cause of these changes had a widespread and dramatic impact. It is not clear whether the cause was climatic alteration, a change in the nature and location of human disturbance or interaction between the two.

Counting the pollen at higher magnification and under phase-contrast, though tedious, resulted in a number of improvements over the initial analysis. The first was the recognition of distinctive pollen types such as Byrsonima which had previously been overlooked and a more realistic appreciation of the number of small or thin-walled pollen types such as Cecropia, Urticaceae and Myrtaceae which had previously been underestimated. In addition to their value as indicators of vegetation, these thin-walled pollen types were also useful in estimating the extent of fossil preservation as conditions altered.

Another improvement was the recognition of a number of Quercus-type pollen which are not in fact Quercus. While specific identification was not possible with the references at hand, general features indicate that these pollen were of the Dilleniaceae and Erythroxylaceae families. By their association with Byrsonima, Quercus, Gramineae and Melastomataceae most of these types appear to belong to Curatella and Erythroxylon species but they are plotted together as "Quercooid".

Terminalia is an arboreal species which is found in flatland forest and bajo areas and whose pollen is very similar to that of Melastomataceae, a fact previously not fully appreciated. Tsukada (1964b) describes Terminalia as being 33 by 24 microns in keeping with other published descriptions. The Melastomataceae are generally smaller though some may reach this size. A cut-off point of 22 microns longest dimension was selected and only one individual grain exceeding this was found in the Quexil core. Specific identification as to species was not possible but the Melastomataceae are almost exclusively limited to the thorn-scrub belt surrounding savannas.

The most difficult anemophilous group to deal with is the Urticales group comprised of the Urticaceae, Moraceae and Ulmaceae. The Ulmaceous types are quite distinctive and are even more so under higher magnification as are some of the Moraceae such as Ficus and Cecropia but the rest are essentially similar. Under high magnification and phase-contrast, many of the smaller and less complex types which normally would be missed are evident as is the fact that the Moraceae and Urticaceae present a spectrum of pollen types within which identification of genus is extremely difficult. Essentially the spectrum is one of what could be termed complexity with variation in size, number of pores, pore structure and exine thickness. It is possible to divide the spectrum into as many units as the investigator may wish yet there is not certainty as to how many species will be contained within each unit.

In the modern vegetation the Moraceae are almost exclusively limited to high forest areas, the exception being those species with distinctive pollen such as Cecropia and entomophilous Ficus. With the exception of the perennial herb Dorstenia, they are trees in high forest and secondary forest.

The Urticaceae range from shrubs to small trees and are more apocentric being found in dry river beds, secondary forest and on steep slopes in open hill forest. From the limited pollen references and published materials for this group, Urticaceae pollen fall at the low end of the observed spectrum and Moraceae towards the high, being more complex by the criteria employed. Further, within the Moraceae there appears to be a tendency for those species found in secondary forest such as Trophis and Castilla to have less complex pollen than those in high forest such as Pseudolmedia. Brosimum, a tree found associated with Mayan sites, whose distribution is believed to reflect Mayan arboriculture (Puleston, 1968) has pollen which falls towards the middle of this spectrum.

Urticales pollen was divided into those which were distinctly Moraceae, distinctly Urticaceae and those in the middle of the spectrum which could not be assigned to either with confidence. The latter group was added to the Urticaceae and the sum plotted in the diagrams as "Urticales" though its interpretation is difficult. If the relation between pollen complexity within the spectrum and plant type is at all valid, then this grouping should represent those species which are the most apocentric of the Urticales and would be found in successional stages. Denslow (1978) suggests that, for tropical vegetation, succession may take place through the temporal partitioning of resources among similar and closely related species, a suggestion also made by Gomez-Pompa, del Amo, Vasquez-Yanes and Butando (1976) for a group of species in the genus Piper (Piperaceae). This method of dealing with the Urticales pollen rests on a similar suggestion with the added

hypothesis that such a temporal partitioning may also be reflected in increasing complexity of the pollen within this discrete group.

Further investigation of Urticales pollen references and surface spectra from different areas will best test this hypothesis though a modest attempt to do so was made in this study. A random 20-25 per cent of the Urticales pollen at each level was subdivided into 20 groups based arbitrarily on complexity. These were scaled such that a mean index of Urticales complexity from 1 to 10 could be assigned to each level. The changes in the Urticales complexity (Figure 7) bear an inverse relation to indications of disturbance, particularly the curve for Ambrosiae pollen. This relation may result from changes in the proportion of successional Urticales species present. Species with distinctive pollen such as Ulmaceae, Cecropia and Ficus were not included in this index.

A last point concerning the use of higher magnification in pollen counting is rather the reverse of the previous ones in that such a technique will tend to underemphasize those larger grains which are important indicators of disturbance but are a small proportion of the pollen rain. The initial pollen analysis was far more successful, despite lower pollen sums, in demonstrating the continuous human disturbance down to the 530 cm level as indicated by Ambrosiae and Compositae. It is therefore recommended that where disturbance may be a factor, tropical palynologists perform separate counts at high and low power.

In order to clarify the meaning of the pollen curves, pollen were grouped according to modern species distributions. In the relative diagram for Lake Quexil (Figure 5) from the left are found "High

forest" which includes those pollen types restricted to this association (Achras, Bombax, Thouinia and Sapium), "Dry forest" with the same relation (Matayba and Alchornea) and "Other AP" which includes those arboreal pollen types previously discussed as being the most adaptable (Sapotaceae, Spondias, Bursera and other arboreals). "Bajo AP" is made up of Haematoxylon and Coccoloba which are almost exclusively restricted to bajo areas. Subsequent groups "Moraceae", "Urticales" and "Quercoid" have been discussed and it should be noted that Moraceae is plotted at half scale.

"Disturbance" is composed of the pollen of Trema, Myrtaceae, Solanaceae and Caryophyllaceae. In later diagrams, Trema is plotted separately as is Myrtaceae in the final Quexil influx diagram. The Caryophyllaceae are a distinct indicator of human disturbance but their pollen is very rare while the Solanaceae are a more diverse group of shrubs, vines and herbs including the tomato, Lycopersicum esculentum. Other members of the Solanaceae are found as shrubs and herbs in cultivated and abandoned clearings and in secondary bush. Trema is a small tree common in secondary forest covering abandoned fields. The Myrtaceae are locally composed of shrubs and small trees found in undisturbed forest some of which, such as Pimenta and Psidium, are selectively encouraged in inhabited areas as ornamentals and for their fruits. They are here used as indicators of disturbance since without such encouragement they would be extremely underrepresented in the pollen rain due to the physical constraints on dispersal of the pollen of understory shrubs imposed by undisturbed forest.

"Savannah herbs" (later "Savannah NAP") is composed of the pollen of Ericaceae and Polygalaceae indicative of well-drained grasslands. "Other NAP" is self-explanatory and "Exotics" includes those pollen types such as Liquidambar, Myrica, Alnus, Ulmus, Carpinus and Podocarpus not found at present in the area. The Pinus is believed to be derived from the Pine-Oak savanna woodland in Northern Belize probably along with an unknown portion of the Quercus pollen. In the AP/NAP representation on the left of the diagram, "Grassland Arboreal" (later "Savannah AP") is the sum of Quercus, Byrsonima and "Quercoid" pollen.

Pollen groups in the relative diagram for the Lake Sacnab core (Figure 6) are the same except that Trema is separated from "Disturbance" and no Ericaceae were observed so Polygalaceae is plotted rather than "Savannah herbs". The diagram also includes the physical stratigraphy and the distribution according to size of the carbonized fragments. The vertical scale has been adjusted to compensate for the 3-1/2 meters of clay deposited during the period of Maya disturbance. This rapid clay sedimentation results in a very low abundance of pollen which are also badly worn due to mechanical abrasion. Such abrasion explains the lack of large carbonized fragments present.

The resemblance to the Quexil core is particularly evident in the Moraceae, Ambrosiae, Gramineae and Compositae curves. Pinus, outside the sum, is also similar and offers an outside reference for stratigraphic comparison between the cores.

The obvious equivalents are:

<u>Sacnab (cm)</u>	<u>Quexil (cm)</u>	<u>Indicator</u>
100	90-100	Moraceae, Gramineae, <u>Pinus</u>
280	170	Gramineae, Ambrosiae, <u>Pinus</u>
390	220	Ambrosiae, <u>Pinus</u>
520	320	Moraceae, Gramineae

The equivalent in Quexil of the bottom of this core is difficult to assess but appears to be between 4 and 5 meters.

The sequence differs from Quexil's in the following ways:

- 1) Its relative lack of Melastomataceae; savanna arboreal species are also generally low (with the exception of Quercus which may have its source in Belize) except at the 280 cm level.
- 2) A greater proportion of Gramineae immediately preceding the Ambrosiae rise (340 cm).
- 3) Significantly greater proportions of Mimosa, Cyperaceae and Cheno-Am, particularly in the lower sections.
- 4) While Ambrosiae and Compositae reach comparable proportions, other disturbance indicators do not.

One of the most interesting stratigraphic features is the association between increases in grasses and clay as opposed to that between Moraceae and gytja in the lower sections. Cheno-Am and Mimosa tend to parallel the former as does bajo arboreal pollen. Differences between the two cores are believed to largely represent vegetational changes in present day bajo areas as opposed to present day savanna areas yet it is difficult to derive specific interpretation of the

Sacnab core. It functions best as a needed reference for the differentiation of regional versus local changes in the interpretation of the Quexil core.

While savanna appears to have been a consistent form of vegetation which may be conceptually related to modern observation, no such assumption appears possible with regard to present day bajo areas. It is likely that these areas were not similar to present day previous to the extreme clay erosion caused by the Maya.

The present day characteristics of bajo areas are mainly caused by the clay soil and it seems likely that much of this clay dates from Maya times, if the extent of clay deposits in the Yaxha and Sacnab deep water sediments is any indication. In both of these lakes, present day inflow, where definable is through bajo areas. Undoubtedly these low-lying areas have always been drainage pathways and thus subject to loads of eroded materials. In terms of the effect on vegetation, a relatively low rate of clay erosion and correspondingly higher proportions of organic matter in the bajo area soil derived locally or through erosion, would result in markedly different vegetation than at present as a result of altered soil drainage conditions. This appears a realistic assumption since bajo arboreal species tended to reach appreciable proportions only during the post-Maya period in the Sacnab area.

The exact nature of vegetation on bajo areas previous to the Maya is obscure yet if one assumes that it causes many of the observed differences between the cores, it appears to have been a low-lying area dominated by bank associations and perhaps grassland scrub. One pictures a mosaic of ponds and badly drained bank and grasslands perhaps

somewhat similar to the pattern of vegetation on the isthmus separating the two lakes today. Any more satisfactory interpretation is strongly constrained by the poor pollen representation throughout the sediments of those species which would be most indicative: the escoba and botan palms.

Bajo areas today are made up of a great number of vegetation types, the distribution and proportions of which are due to drainage conditions. If similar relations existed in the past in these areas, under altering climatic or human disturbance, one may only suppose that each such vegetation type will have been altered in an independent manner.

The pollen diagram for Lake Quexil shows the most impressive feature in 8000 years of local environmental history to have been Mayan disturbance and deforestation. Forest removal reaches a maximum at 170 cm and, while reforestation continues upward from this point, it is constrained until apparent abandonment at the 85 cm level. Being also observed in the Sacnab and Peténxil cores, it is evident that this was a regional feature.

The other major feature is the expansion of savanna as indicated by Gramineae, Melostomataceae and the grasslands arboreals reaching a maximum around 200 cm. This expansion is associated with a decreasing proportion of large carbonized fragments (Figure 9) indicating that rather than establishment of a local belt surrounding the lake, savanna expanded over an increasingly broad area. The decline of Melastomataceae at 220 cm and the subsequent increase in grassland arboreals suggest a degree of reforestation taking place which is somewhat inconsistent with the increasing human disturbance indicated by the Ambrosiae and Compositae curves. Details such as this, as well as

the actual proportion of change generally, may be strongly affected by the fact that this is a percentage diagram. The dominance of Moraceae in the lower section, forming 80-90 per cent of total pollen with Urticales, is a text-book example of the restrictions imposed by a relative diagram. As a result of this dominance, all other curves are suppressed to the point where interpretation is hazardous without an influx diagram. In effect, the apparent expansion of savanna may simply be a mathematical artifact resulting from the removal of such suppression.

An influx diagram can only be as accurate as the dating control particularly where there have been short term changes in the conditions and rates of sedimentation. Such changes are suggested by the physical stratigraphy as well as similarities between the density curves for pollen and the aquatic fossils, (Figure 8, Figures 14 and 15 in the Appendix). Combined with the lack of certainty of ^{14}C dates in the limestone area, this makes it unlikely that a perfectly accurate influx diagram is possible. Both relative and influx diagrams therefore have their weaknesses as well as strengths and interpretation of past vegetational changes depends on both.

A further complication is introduced by variations in diagenesis particularly in those sections dating from the Classic period when the anthropogenic sediments are rich in silicate and carbonate. Changes in the severity of post-depositional destruction of microfossils cannot be distinguished except by implication from actual vegetational or lacustrine alterations when the recognition of such alterations depends on counts of remains varying in their susceptibility to such destruction.

Using dating assumptions similar to those in this study, Brenner (1978) demonstrates that the calculated influx of all fossils is charpely reduced during the Classic and Postclassic periods in the sediments of Lakes Yaxha and Sacnab and, to a lessor extent, Lake Quexil. He concludes that the cause is post-depositional destruction yet other factors may also be involved. The first might be an error in the dating estimates which would alter all influx rates. There is no reason at present to suppose an error of sufficient magnitude to have been made though doubtless minor errors are present. The second factor might be that the lower influx rates may, at least in part be due to low lake productivity, possibly as a result of increased turbidity, and/or vegetation dominated by entomophilous species.

For pollen, severe diagenesis is indicated by the presence of visibly degraded grains with the corollary that pollen types which are more fragile than those so observed may have been completely destroyed. There is no doubt that this is the case in the clay layers in the Sacnab core. All pollen is visibly degraded in a distinctive manner which indicates fine mechanical abrasion. As a result, the proportions of the finer grains such as Cecropia, Byrsonima, Melastomataceae and Urticales must be considered as minimal estimates. Further, variations in diagenesis within the clay layers might alone cause stratigraphic changes in the proportions of these fragile pollen types. Since it may be observed in Figure 6 that peaks of Cecropia, Byrsonima, Melastomataceae and Urticales are not coincident in the clay layers, actual vegetational changes appear to be represented, however inadequately.

The same is not true for the Lake Quexil core, however, whose sediments during the equivalent period are not so dominated by clay. Here not only is pollen not visibly degraded but the curve for Urticales complexity (Figure 7) clearly indicates that the more fragile grains increase in proportion during this period, an observation in direct conflict with the occurrence of increasingly severe post-depositional destruction of pollen.

Pollen is generally less fragile than planktonic fossils and this observation does not demand alteration of Brenner's (1978) conclusion that influx rates of the fossil types based on counts of remains do not reflect production rates of plankters during this period. The point is that at no time in the Quexil core are there indications that post-depositional destruction was so severe as to cause significant changes in the pollen present. As in all such studies, the possibility cannot be totally eliminated but, lacking such indications, interpretation must rest on the initial assumption that changing rates of pollen influx in the Quexil core reflect real vegetational changes.

On the left of the relative pollen diagrams of the Quexil and Sacnab cores are the uncorrected ^{14}C dates. Those for Lake Quexil were performed at the Radiocarbon Laboratory of Dalhousie University and those for Sacnab at the Quaternary Research Center of the University of Washington. With the exception of the bottom-most in Quexil which is based on a sample of lake deposited wood (DAL 198, 8410 \pm 180, Dalhousie II, Ogden and Hart, 1977), all others are subject to a degree of carbonate error the extent of which, if in any way systematic, is at present elusive. All hypotheses based on a constant error,

inclusion or non-inclusion of specific dates and comparison between cores result in some form of conflict with other evidence. One example may be seen in Figure 7 where the calculation of pollen influx based on four uncorrected dates for the Quexil core clearly shows a massive extent of sediment redeposition between 2 and 5 meters. If correct, such sediment should be rather homogenous and this is seen not to be the case by the stratigraphy of the aquatic fossils, plant macro-fossils, total phosphorous and carbonized fragments. Such an hypothesis further conflicts with the bottom date of the Sacnab core and for these reasons, amongst others, must be judged untenable. Dating control is therefore based on the bottom date of the Quexil core and on the Mayan archeological sequence and its relation to observed changes in pollen and chemical stratigraphy.

Correcting the Quexil bottom date for the Libby half-life and Suess's correction for atmospheric ^{14}C , yields a calendar date of approximately 9400 BP. Initial indications of human disturbance at 530 cm are assumed to be coeval with the early Swasey Phase in Belize and estimated at 5000 BP. Considering the population estimates from the Yaxha-Sacnab basin and the effects on land use, the 310 cm point of inflexion in the rate of deforestation implied by the Moraceae curve is estimated to occur at the Middle Preclassic to Late Preclassic boundary at 2220 BP.

The upper portion of the bimodal Ambrosiae curve is assumed to represent Postclassic populations since they are otherwise unrepresented but it is difficult to know whether to place the Classic Maya collapse at the lower Ambrosiae maximum at 170 cm or at the 140 cm

minimum. On the basis of the Moraceae curve, maximum deforestation occurred at 170 cm with reforestation taking place between 170 and 140 cm. The collapse of 1070 BP was therefore estimated to be at the 170 cm level and this further suggests that depopulation took place in a gradual manner in agricultural areas as opposed to the apparent suddenness in urban areas.

Comparing the time of the final decline of Ambrosiae using the Pinus curve for reference indicates that depopulation took place at a similar time in the basins of both lakes. Certainty of this, and thus insight into the question of location of Postclassic Tayasal, would depend on an increased number of levels studied in Sacnab but pending this, the Ambrosiae decline at 85 cm in Quexil is estimated to have taken place at the time of Spanish conquest at 270 BP.

Figure 8 shows the Depth/Age curve derived using these estimates and the sedimentation rates which are:

0-85 cm	.3148 cm/yr.
85-170 cm	.10625 cm/yr.
170-310 cm	.12173 cm/yr.
310-530 cm	.07914 cm/yr.
530-623 cm	.0227 cm/yr.

In the center of Figure 8 is the Mayan archeological sequence with the dating estimates used in solid lines and dashed lines marking the locations of the standard divisions as derived from the Depth/Age curve.

These sedimentation rates are used with the pollen density to derive the total pollen influx shown in Figure 9 as the raw influx and the influx smoothed by use of a running mean of three adjacent values.

The latter was used for the calculation of the influx diagram (Figure 10). To the right of the averaged pollen influx are the carbonized fragment influx with the percentage *Ambrosiae* curve for reference, the relative size of the carbonized fragments and the influx of the larger carbonized fragments. The carbonized fragment influx for the Lake Sacnab core was calculated by using the depths of apparent equivalence between the two cores previously mentioned. The dates of these depths on the Quexil Depth/Age curve were used to derive the sedimentation rates for the Sacnab core:

0-100 cm	.250 cm/yr.
100-280 cm	.2687 cm/yr.
280-390 cm	.2292 cm/yr.
390-520 cm	.1530 cm/yr.
520-636 cm	.0468 cm/yr.

The bottom date for Sacnab, used to derive the last sedimentation rate above, is based on assuming a 2,010 year carbonate error in the bottom-most ^{14}C date (6410 ± 100 BP). Corrected for Libby half-life and atmospheric ^{14}C , this gives a calendar date of 4750 BP, equivalent to the 510 cm level of Quexil. The carbonized fragment influx for Sacnab is plotted according to the age scale at the far left of the figure and is remarkably similar to that for Quexil particularly in the maximum observed around 1500 BP. In contrast to Quexil, however, this maximum in Sacnab is associated with an increased proportion of large fragments and minimal *Melastomataceae* (Figure 6).

The original pollen percentages were applied to the averaged pollen influx to derive the values in the Quexil pollen influx diagram (Figure 10).

Figure 4: Lake Sacnab Core 1: Physical Stratigraphy and Loss on
Ignition

LAKE SACNAB, PETEN, GUATEMALA

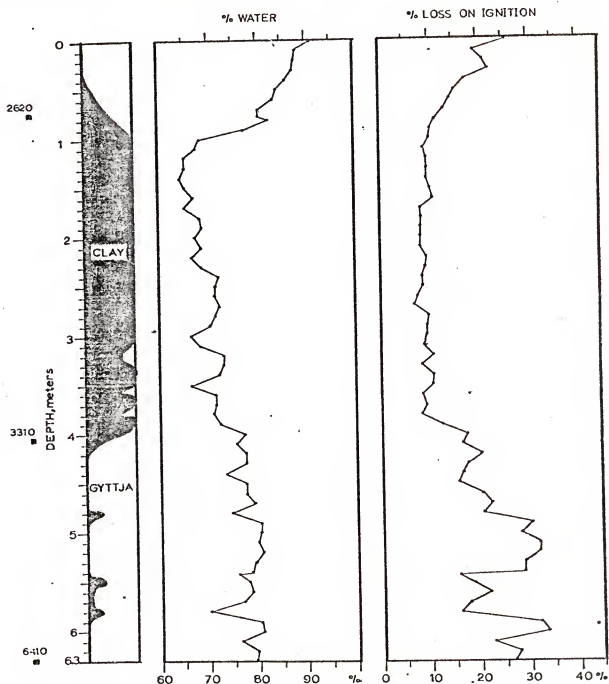


Figure 5: Lake Quexil Core 1: Relative Pollen Diagram

RELATIVE POLLEN

LAKE QUEXIL, PETEN, GUATEMALA

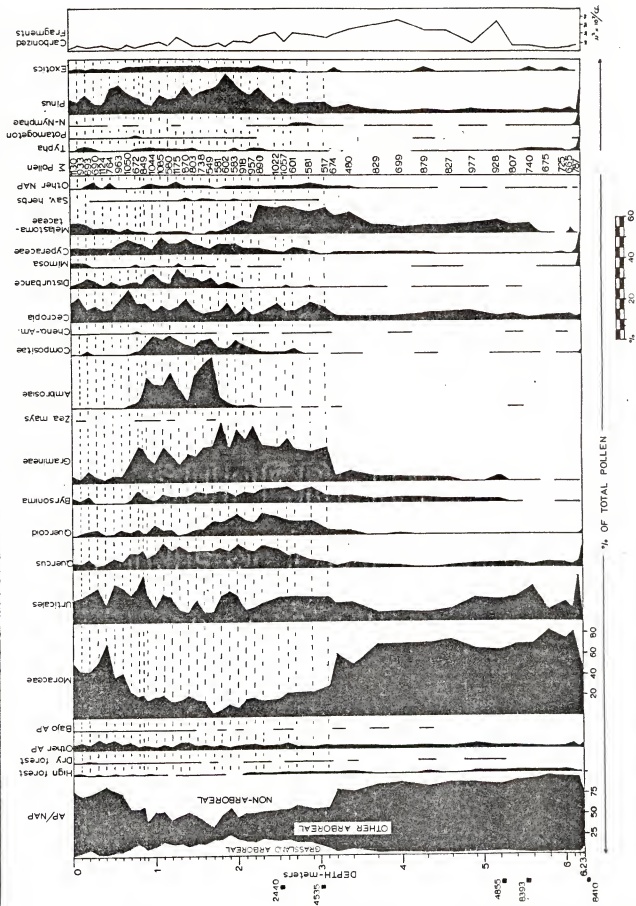


Figure 6: Lake Sacnab Core 1: Relative Pollen Diagram

LAKE SACNAB PETEN GUATEMALA

RELATIVE POLLEN

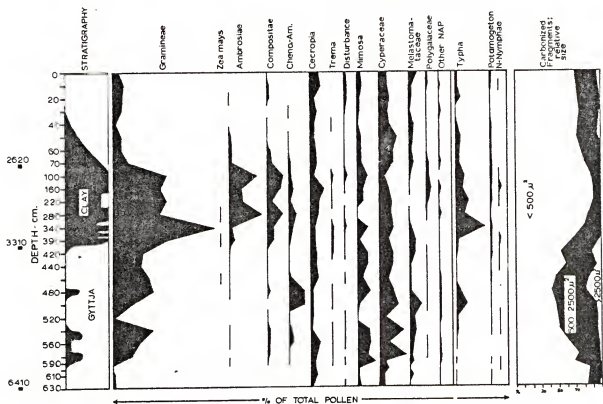
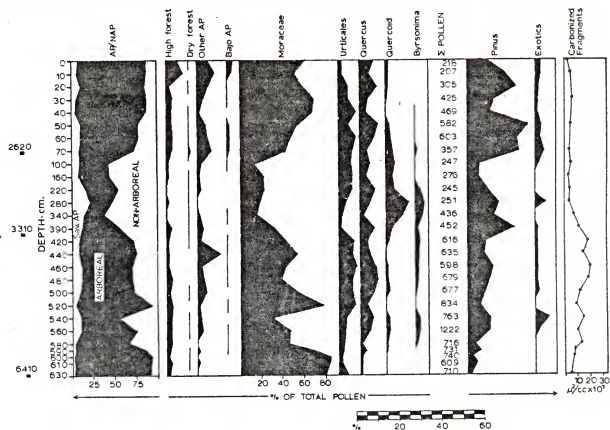


Figure 7: Lake Quexil Core 1: Carbonized Fragments, Urticales Complexity
and Initial Approximation of Pollen Influx

LAKE OUEXIL, PETEN, GUATEMALA

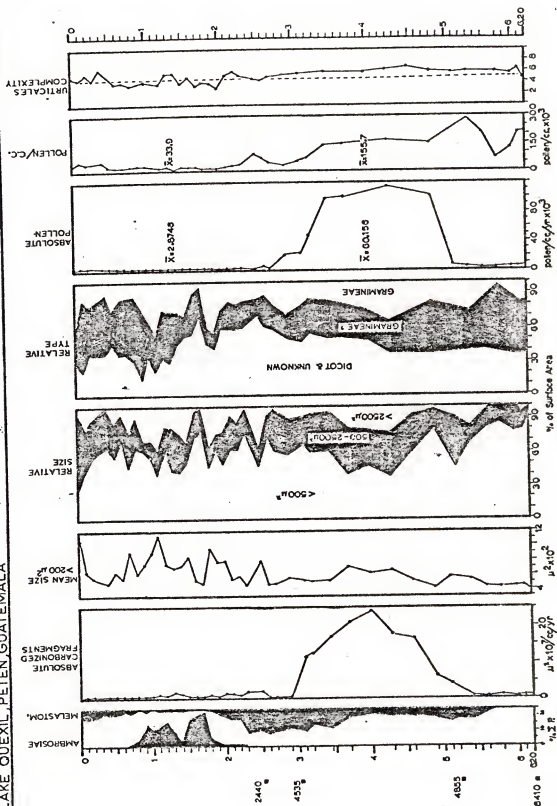


Figure 8: Lake Quexil Core 1: Physical and Chemical Stratigraphy,
Derivation of Depth/Age and Sedimentation Rates

LAKE QUEXIL, PETEN, GUATEMALA

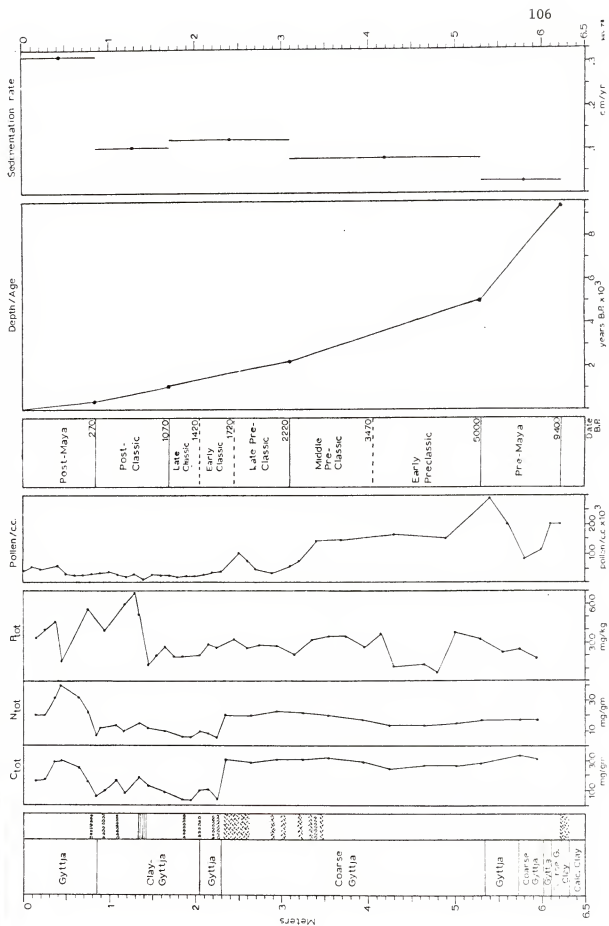


Figure 9: Lake Quexil Core 1: Total Pollen and Carbonized Fragment Influx
Lake Sacnab Core 1: Carbonized Fragment Influx

LAKE QUEXIL, PETEN, GUATEMALA

LAKE SACNAB

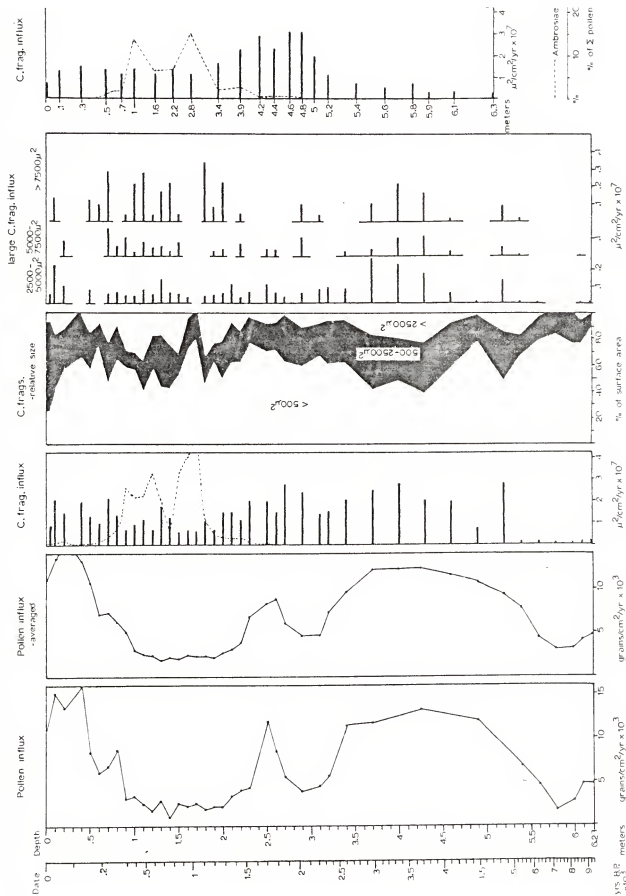
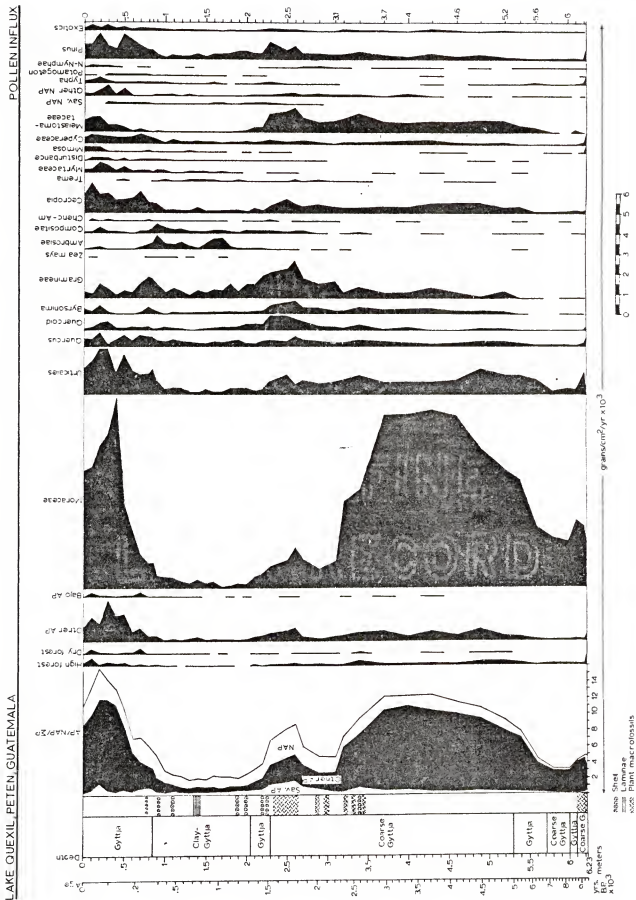


Figure 10: Lake Quexil Core 1: Pollen Influx Diagram



DISCUSSION

In interpreting these results one must first assume that the archeological data from the Yaxha-Sacnab basins demonstrate general features which are common to other local basins particularly the population densities, preference for upland areas and increasing centralization. There is little reason to question this assumption for the earlier Mayan periods but beyond a certain point of land use intensification and centralization, patterns of land use, settlement and population density may have differed between basins whereas previously these had differed mainly within the basins. As centralization increased, so must the scale of these patterns such that by Classic times, basins may have differed in being predominantly urban, suburban or agricultural. The observation of higher levels of Moraceae during the Classic and Postclassic in Sacnab than in Quexil, for example, may be a result of such differentiation.

Prior to indications of human disturbance, the Quexil influx diagram mainly shows variations in the Moraceae influx, being higher in the coarse gyttja with macrofossils section from 610-623 cm and declining in the gyttja section from 600-610 cm. Large carbonized fragments and Melastomataceae are present in the former though not in the latter. Similarly Gastropods are present in the 610-623 cm section whereas Pediastrum and Desmids occur in the 600-610 cm section. Data is minimal but sufficient to suggest alterations in lake level

and climate during this period. At the bottom-most levels, dominance of Typha, Nuphar-Nymphae, Cyperaceae and Mimosa suggest a shallow pond with a bank association increasing in depth to the gyttja zone of 600-610 cm. Melastomataceae and carbonized fragments suggest the presence of fire implying either lower rainfall or a drier and/or longer dry season than occur in the 600-610 cm section.

Some features are repeated between 530 and 600 cm with the gyttja zone between 530 and 570 cm again being associated with Pediastrum and Desmids as well as Diatoms, all not observed in the coarse gyttja between 570 and 600 cm. Terrestrial conditions are, however, different. Though again Moraceae and Melastomataceae expand in the coarse gyttja section, large carbonized fragment influx does not. In fact the previous trend is somewhat reversed with large and total carbonized fragment influx increasing in the upper level of the gyttja section during which Moraceae and Melastomataceae continue to increase. If one assumes that there is no human disturbance at this time then the presence of carbonized fragments and Melastomataceae may be taken to indicate a drier and/or longer dry season, i.e., increased seasonality as previously defined. Changes in the lacustrine system, however, appear to be due to alterations in lake level with the gyttja sections representing periods of deep and/or stable levels and the coarse gyttja the reverse. If that is the case, the lake level record is similar to that described by Sarnthein (1978) for the tropics generally, based on lake levels and dune formation, with periods of "humidity" at 10000 - 7500 BP and 6500-5000 BP. A better fit is possible if one assumes that the lower-most coarse gyttja section is simply due to a slow initial

filling under overall humid conditions. This similarity also tends to support the dating estimate for the 530 cm level. The data on Melastomataceae, Moraceae and carbonized fragments suggest that the climatic pattern was more complex but are insufficient to demand modifications of Sarnthein's general pattern. More detailed investigation of the suggested complexities in this section in future may be able to answer the question of why this pattern is not so apparent in Florida or Panama.

Above 530 cm vegetation may be presumed to be subject to exponentially increasing human disturbance. The most remarkable immediate change is the continued increase of Moraceae influx to the 370 cm level. Lacking indications of other forms of vegetation in related decline, it appears that this represents an increasing dominance of Moraceae within existing forest formerly dominated by entomophilous species such as the Legumes. The maximum Moraceae influx (370-460 cm) takes place associated with high influx of large carbonized fragments (Figure 9) and without the presence of plant macrofossils which are present during the subsequent steep Moraceae decline. Increases in Cecropia, Trema and Urticales are indicative of forest succession while increases in the adaptive "Other AP" suggest that forest was being exploited in a patchy manner with these species being favoured at forest edges. It appears that disturbance was altering the forest composition either through altered soil conditions resulting from the nature of the disturbance or by allowing the expression of the prevailing climate in successional stages which otherwise might not have been expressed due to vegetational inertia. At the same time savanna

increased in the area as shown by the concurrent increases in Melastomataceae, Gramineae and the savanna arboreals from 540 cm to 370 cm.

It also appears that the carbonized fragments present during this period were derived from grasslands rather than from slash-and-burn agriculture in forest areas (Figure 7) though generally the differentiation of carbonized fragments as to type did not yield results which can be conclusive. As shown in Figure 7 by comparison of the curves for Gramineae type fragments and for mean size, the ability to differentiate as to type is largely a function of the size of the fragment: the greater the mean fragment size of a sample, the greater the proportion of distinctly Gramineae type observed. As a result, the greater the distance of the source, the lower the proportion of Gramineae type would be, even if the same type of vegetation is burning. Further, as discussed in the section on carbonized fragments, woody tissues are more likely to result in small fragments when burnt so that all large particles will tend to be Gramineae. Therefore on the two levels where Gramineae type are lacking (170 cm and 580 cm) either all fires are at a distance or there are no grasses being burnt. The presence of Gramineae type in all other levels does not necessarily indicate grassland burning since grasses are present to some extent in almost all local forms of vegetation except undisturbed upland forest. As land use intensity increases, one may therefore expect that it is increasingly difficult to differentiate on the basis of fragment type between naturally occurring grassland fires and the burning for agricultural purposes of previously disturbed areas. As a result there is disappointingly little that can be interpreted from the relative type analysis of the carbonized fragments in the upper half of the core.

In the section 370-540 cm, population density was low enough that agriculture was probably being practised in fully forested areas and therefore agricultural burning is unlikely to have resulted in Gramineae fragments. One may safely conclude that the carbonized fragments present are derived from burning savanna whether due to natural fires or human disturbance.

During this period, the proportion of savanna remains fairly constant and the high influx of large carbonized fragments suggests that it is quite local. It was therefore probably restricted to the area of poorly drained silty clay soil to the south of the lake and the concurrent presence of Ambrosiae, Compositae, Cheno-Am, Myrtaceae and "Disturbance" pollen at the 540 cm level may indicate the disturbance of this immediate area which resulted in savanna. What form of vegetation this area supported previously is unknown except to the extent that it was either forested or dominated by entomophilous species.

During this same period in the Sacnab basin, represented by the section 590-630 cm of the Sacnab core, large carbonized fragments are low or lacking as are savanna indicators. Cecropia and Urticales are present indicating some disturbance of upland forest areas though "Other AP" are present only at low levels. The pollen may, however, all be at low levels because of the percentage dominance of the Moraceae and any interpretation of the relative degree of land disturbance between the two basins is therefore not justified. The presence of savanna is, however, not indicated.

Given that savanna during this period is largely restricted to the southern shore of Lake Quexil, the questions remain as to its cause and maintenance. The influx of Gramineae in Quexil varies with

the influx of large carbonized fragments, being high at 520 cm and 420 cm, and these may represent either climatic alterations or attempts at exploitation of savanna. Population levels were not so high as to warrant repeated attempts to exploit the savanna areas so it may be presumed that the fires were natural and that climate was such as to maintain a savanna on this particular soil type without continuous human disturbance though such disturbance may have been necessary for its inception. Climate was also such as to cause an increased dominance of Moraceae in other disturbed areas.

A further indication of conditions is the high C/N ratio observed in the sediments. Lacking pollen evidence for local bog or bajo vegetation, this indicates either low lake level and the proximity of a littoral zone or altering lake levels resulting in transport of sediments from a more distant littoral zone. The decline of Typha tends to indicate the latter while the increases in carbonized fragments influx and the continued presence of low levels of Nuphar-Nymphae suggest that alteration is occurring on a seasonal basis rather than between years. This is consistent with the self-maintaining savanna area but the meaning of the increasing Moraceae dominance is less certain.

For the Atlantic coast of Panama where the dry season is far less pronounced than Guatemala's, Bartlett and Barghoorn's (1973) analysis of surface samples show about 22 per cent Urticales described as mainly Moraceae such as Ficus and Cecropia and Trema of the Ulmaceae. Modern pollen spectra in Quexil show about 80 per cent of the pollen to belong to the Urticales. This is a somewhat less than satisfactory comparison since the methods of analysis were not the same, nor is seasonality or dryness by any means the only difference.

Gomez-Pompa (1973), in describing the vegetation of Veracruz, shows increasing dominance by the Moraceae in moving from evergreen high forest to semi-deciduous high forest. This suggests that it is consistent that Moraceae influx should increase under conditions of increasing seasonality or dryness but again the comparison is less than satisfactory. What is required is analysis of surface samples from various areas and even then the point may not be certain unless there are sufficient numbers of them to separate the variable of seasonality or dryness from those of soils, history, temperature, etc.

Evidence cannot therefore be considered conclusive but it appears that the period 3000-5000 BP was one of increasing disturbance of upland areas under a climatic regime that was more seasonal or drier than that previously.

In the Quexil section 310-370 cm, the dominant change is the decline in Moraceae taking place between 2200 and 3000 BP in the Middle Preclassic. It is not clear what is replacing the Moraceae, increases in savanna and successional species being slight in proportion. During this period plant macrofossils increase in the sediments, influx of large carbonized fragments decline and total carbonized fragment influx declines slightly. The major factor at work was increasing population reaching densities which may have forced the beginnings of more intensive land use yet there are no indications here that such intensification involved shortening fallow cycles or any increasing amount of successional areas involving anemophilous species. Were human populations not increasing, this change in the Moraceae might be interpreted as a change in forest composition involving increasing proportions of entomophilous arboreal species in areas after

disturbance similar to, though the reverse of, the type of change hypothesized for the earlier Moraceae increase. Such a change need not be associated with increasing indicators of forest succession, only their persistence at a moderate level. Human populations were increasing, however, and the continuation of the Moraceae decline from this point through the Classic period indicates that this represents deforestation, an hypothesis consistent with the decline in "high forest" and "Other AP" during the 230-370 cm section. If this was the case, the lack of related increases in forest successional types or in Gramineae, Cyperaceae or others which might indicate shortened fallow cycles suggest the direct replacement of Moraceae by underrepresented vegetation. One way in which this may have occurred is if intensification took the form of continuous exploitation of preferred upland areas by methods such as inter-cropping rather than alterations in the intensity of slash-and-burn monoculture or the exploitation of less desirable areas. If the observation of the use of both maize and root crops in the early Swasey phase is correct, then such a form of intensification need not involve the type of quantum jump necessary in going from monoculture to polyculture. The observation of public architecture and distinct socio-political zones in the Yaxha-Sacnab basin during this period indicates that unknown factors of custom and law may have affected or limited available choices. Further, the continued preference for upland areas in the settlement pattern lends support to this land use hypothesis. This is not to say that exploitation of upland areas suddenly altered to continuous polyculture nor that these were the only areas utilized. The continuous levels of

Cecropia and Urticales and the increase in Trema demonstrate forest succession taking place in some areas. The slight increases in Melastomataceae, Gramineae, Byrsonima and Quercoid pollen also show savanna to have increased with the declining large carbonized fragment influx indicating that such increase took place at a greater distance from the lake. This increase may have been a result of attempted intensification on flatter areas.

The salient point is that areas dominated by Moraceae were being rapidly transformed into underrepresented vegetation under conditions of increasing disturbance without any increase in the indicators of intervening successional stages. Interpretation depends on the assumptions made as to the location of Moraceae dominated forest and the nature of the underrepresented vegetation. If such forest was on upland areas, then the lack of increase in successional stages would indicate temporal intercropping such that there was no abandonment of upland agricultural areas.

If the Moraceae forests were restricted to flat and gently sloped areas, the other possibility is that the underrepresented vegetation was such that successional stages were also underrepresented. Such a form of vegetation might be low deciduous forest for which there are ambiguous indications discussed later, and would indicate increasing dryness consistent with the 3000 BP dry period documented in Africa. Both hypotheses may have been true, taking place with the limited forest succession indicated occurring on areas between the two extremes. Either or both would tend to reinforce a preference for upland areas.

Comparisons with the Sacnab core must be based on the Quexil relative pollen diagram which, because of the nature of percentage calculations, tends to indicate that forest was being replaced by savanna. The influx diagram shows this not to have been the case and it must be assumed that this apparent relation was not true for Sacnab either. It is nonetheless true that grasses, Melastomataceae and savanna arboreals were present in the Sacnab area during this period (500-580 cm) though their apparent increase may be solely a percentage effect. Low levels of large carbonized fragments indicate that burning was present at a distance.

As percentages, the changes in Moraceae, Cecropia, Urticales, Trema and indicators of disturbances are similar to those observed in Quexil. Percentages of Mimosa and Cyperaceae are higher as an indication of bank associations in the modern bajo areas to the east and northeast. It appears that the patterns of disturbance and land use were similar in both basins.

A feature which is not explained is the sudden increase in Moraceae at 320 cm in Quexil and 520 cm in Sacnab. In Quexil, this increase is visible at only one level and therefore might be ignored as an error but its presence in Sacnab makes it a regional change which requires explanation. In Sacnab, Moraceae suddenly increase from 35 per cent to 80 per cent of total pollen resulting in a decline in all other pollen as a mathematical result. The exception is Urticales. Though the increase is smoothed by the influx calculation in Quexil it still appears to be related to a decline in savanna to levels similar

to those in lower sections. In Quexil, it is observed to be between incidents of high plant macrofossil content and in Sacnab between possibly related clay lenses.

Turning to Gomez-Pompa's (1973) analysis of the ecology of vegetation of Veracruz, one finds that the result of increasing dryness tends to be the "low deciduous selvas" containing elements of the semi-deciduous forest and savanna woodland. It is a very diverse association (Gomez-Pompa, 1973: 121-124) most of whose elements are not anemophilous and, as such, the replacement of Moraceae forest by a similar association in some areas would be indicated by modest increases in savanna, adaptable "Other AP" and "dry forest" pollen. Of the possible explanations for the sudden Moraceae increase, that which is most consistent with all evidence is the existence of some such association on the rolling areas and gentle slopes of Calcimorphic Rendzina soils with a climate which is a continuation of the trends hypothesized for the next lower section and is consistent with the African record. A temporary moist period would then result in expansion of Moraceae in these areas. The existence of such an association in these areas would again be a result of human disturbance in that climate would be expressed through its effects on the successional stages resulting in low deciduous forest rather than high semi-deciduous forest which may have occupied these areas previously. This would also further account for the preference for upland areas in settlement pattern. Any other explanations must hypothesize a coordinated and dramatic change in the pattern of human disturbance for which there is no archeological evidence and which fails to explain the associated changes in sediment. The increasing presence of coarse

macrofossils suggests either the immediate proximity of a stable littoral zone for which pollen evidence is lacking, or increasingly extreme fluctuations in lake level resulting in the transport to the coring site of coarser materials. If the macrofossil layers are concurrent with the clay lenses in Sacnab, as they appear to be, the clay suggests enhanced upland erosion or higher flow rates through bajo areas where such clay might normally settle. A shorter and more intensive rainy season or increased rainfall under a highly seasonal regime is therefore indicated for these periods with a temporary altering of the conditions resulting in increasing dominance of Moraceae in low deciduous forest areas at 2300 BP.

Here, as previously, interpretation of the nature of climate and human disturbance is tenuous but this is a predictable result of the limits of the evidence. As pointed out in the introduction, explanatory hypotheses must be consistent with all lines of evidence, especially when the meaning of any single line of evidence is obscure or ambiguous. The necessary emphasis on the rejection of hypotheses on the basis of conflict within or between lines of evidence does result in interpretation which is heuristic in the Holmesian sense of "when you have eliminated the impossible, what remains, however unlikely, must be true" but such interpretation is disquietingly free of the comfort which pragmatism provides. Some such comfort is possible if the changes in climate and human disturbance hypothesized are systematic rather than being a series of discrete states the relation between which is unfathomable but this is rather dependent on the fundamental philosophy of the investigator as to the nature of change.

The section 230-310 cm in Quexil demonstrates an apparent continuation of previous trends during the Late Preclassic and the first half of the Early Classic. During this period exponential growth of population forced settlement on the slopes and some badly drained soils in the Yaxha-Sacnab basin as well as increased density on upland areas. Total carbonized fragment influx increased in both Quexil and Sacnab though influx of large fragments declined in Quexil and the proportion of large fragments increased in Sacnab. Quexil sediments were increasingly dominated by coarse macrofossils and all indicators of savanna reach a maximum. Cecropia, Urticales, Trema and "Other AP" increase as does Moraceae to a slight degree. The indicators of human disturbance are consistently present from this period to modern time. "Savanna NAP" makes its appearance. Typha and Nuphar-Nymphae reappear and this is the transitional period in the lacustrine system as particularly evident in the curves for Ostracods, Gastropods and Bosmina.

Population density reached a point during this period where all areas must be considered as subject to disturbance of some form yet there are two opposing tendencies in the results. On the one hand, the presence of relatively widespread wooded savanna argues for the exploitation of less preferred soils resulting in savanna due either to the intensity of such exploitation or overall dryness. On the other hand, increases in Moraceae, "Other AP" and successional pollen argue for a slight degree of reforestation or increased dominance of Moraceae on underrepresented areas such as the previously hypothesized low deciduous forest which might indicate moister conditions. Such an hypothesis is in part supported by the re-establishment of littoral

vegetation which, to be consistent with the coarse macrofossils, suggests low but more stable lake levels. If this is the case, it would explain why the Peténxil core, obtained in shallow water, was unable to penetrate sediments beyond this age.

In the Sacnab basin, sediments of this period (420-500 cm) indicate similar changes with a low percentage of Moraceae associated with a clay lens at 480 cm equivalent to the Moraceae minimum at 290 cm in Quexil, and subsequent increases in Moraceae, "Other AP" and Cecropia at 460 and 440 cm where clay is not present. Sacnab differs in having a high proportion of large carbonized fragments, lower Typha and lower Melastomataceae for these levels. Byrsonima and Quercoid pollen increase but this may be a percentage effect, while Gramineae reach similar percentages as in Quexil.

There is a risk of simply making modern bajo areas a catch-all for whatever can't be explained in the Sacnab core yet the existence of this area is one of the fundamental differences between the two modern basins and its history is one of pure supposition. If the interpretation of lower but more stable water levels is correct, a decline in Typha and an increase in Gramineae with large carbonized fragments reaching the directly downwind coring site is acceptable if this area, as previously hypothesized, was a mosaic of pools, seasonal streams, bank associations and other unknown forms of vegetation. The lack of increased Melastomataceae and savanna arboreals may then indicate a grassy vegetation similar to that of upper banks, which may have had Cheno-Am as a constituent whose increase during this period is otherwise unexplained. Persistent levels of Mimosa and Cyperaceae indicate lower bank associations present. The presence of Typha

in Quexil but not in Sacnab under these conditions is consistent with the local topography and bathymetry in that the Quexil coring site is protected from the dominant winds by an island to the east and might have been a separate pond if lake level were sufficiently low while the Sacnab site would still be effected by a long wind-fetch to the east and the lack of wave-protected areas on the shore.

Conditions therefore appear to have been drier but with less variability, either seasonally or between years, than previously. These conditions, along with increased amount and intensity of human disturbance, resulted in increased amounts of savanna probably on flatter areas in the Quexil area.

The increase in forest succession in both basins may be due to a number of factors. One first presumes that this did not take place on upland areas where housing density and land values would make forest succession rather an expensive indulgence. Neither did it probably occur in the flatter areas where disturbance resulted in savanna during this period. It therefore probably occurred on the gently sloped Calcimorphic Rendzina areas. Here again this is an apparently similar situation as that of the Moraceae increase at 320 cm with essentially the same possibilities: either a co-ordinated and dramatic change in exploitation strategies or climate affecting the results of disturbance. There is insufficient evidence for a confident choice. Altered human disturbance does not explain the changes in sediment or the lacustrine system or the littoral zone yet to ascribe the increases to climate, it is necessary to invoke underrepresented vegetation such as low deciduous forest. The increases in forest succession and Moraceae around 250 cm might then be due to the lessened variability.

The entire period 1500-5000 BP in the area is a difficult one to interpret in detail yet a few generalities are apparent. Though initially human disturbance may have occurred on the flatter area to the south of Quexil, resulting savanna-ization reinforced a tendency for settlement on more productive upland soils. As population increased, so did exploitation of less preferred areas with the result of such efforts, and thus probably exploitation strategies, increasingly differing according to the nature of the area. It is this tendency towards increasing differentiation between areas making the area as a whole more diverse vegetationally that renders interpretation difficult. There are no indications that the process of land use intensification was in general one of decreasing fallow cycles though this may have occurred at specific times, on specific areas or in connection with specific crops.

Climatically, the period was one of increasing dryness at least one component of which was the variability indicated by changing lake levels and grassland burning. Such variability may have taken the form of increasing between year variation or increasing seasonality and appears to reach a maximum between 2000 and 2800 BP. The period 1500-2000 BP appears to be one of decreased variability but lower total rainfall. While these changes affect lake levels and littoral development directly, their effect on vegetation is less straightforward since their point of impact is the successional stages. The vegetational expression of climate was therefore primarily a function of the specific nature and location of human disturbance. For example, it is impossible to say that the maximum spread of savanna at

1800 BP was a climatic effect since it may not have taken place if disturbance of the previous vegetation had not occurred. It is equally impossible to say that it was an effect of disturbance since it may not have occurred if climate were different. To attempt to say either would betray a profound misunderstanding of the processes involved since the changes observed reflect the state of the total system of which climate, vegetation or land use are components none of which are independent or static. While it may be well argued that climate is independent, its effects are not.

The history of this total system during the period 1500-5000 BP may be considered as driven by the forces of climatic alteration and increasing population apparently resulting in shifting patterns of land use and vegetation both of which increased in diversity over the area as a whole as a result of both becoming increasingly specific to the features of any one site.

In the Quexil section 170-230 cm there is clear evidence that all areas of the Quexil basin were subject to increasingly permanent use. All indicators of primary and secondary forest declined steadily to the point of almost non-existence by the time of the Maya collapse. Ambrosiae increases exponentially while other indicators of disturbance are continuously present. Trema, Cecropia and Urticales are present though strongly attenuated. None of this is particularly surprising considering the population densities observed in the Yaxha-Sacnab basin though the extent of deforestation, being almost total, would be a source of amazement to an observer of the area today. The manner in which savanna declines does, however, merit some consideration. There are no indications that this decline was natural in a way

which might be consistent with what is known of savanna. Such a natural decline would first involve an increase in savanna arboreal species and here it may be observed that all indicators decline together suggesting human utilization or physical occupation. These changes need not have involved any climatic alteration, merely increased human effort.

For the Lake Sacnab basin, similar trends are indicated for forest areas, though Moraceae does not reach as low a percentage as in Quexil. This may be due to less intensive land use.

The two cores differ in the changes in the savanna indicators as viewed through comparison with the Quexil percentage pollen diagram. One may observe in the Quexil relative diagram that the decline in Moraceae alters the apparent relation of savanna as a percentage effect. It appears that Gramineae persist at a high level and the maximum of the savanna arboreals occurred around 190 cm. The influx diagram demonstrates that this is not in fact the case. Similarly, in Sacnab, Gramineae and the savanna arboreals appear at higher levels but Gramineae increase through the Classic and Postclassic and the savanna arboreals reached their maximum at 280 cm, the time of the Classic collapse as indicated by Ambrosiae. This is later than in Quexil. The record for Melastomataceae is, however, similar. This may be entirely a percentage effect, differing from Quexil due to the higher levels of Moraceae which persist, but does suggest the transformation of some flatter areas to savanna during the Late Preclassic and Early Classic as in Quexil. The proportion of this apparent later persistence of savanna may however be due to less intensive land use which did not demand the kind of effort which exploitation of savanna requires. It is difficult

to be certain of this without an influx diagram for Sacnab which was found impossible to produce with any confidence. One may however entertain the possibility that population density was higher in the Quexil basin during this period than in the Sacnab basin.

Indicators of disturbance are, in general, similar in both basins though detailed comparison is constrained by the low pollen count, distance between levels and poor pollen preservation in Sacnab resulting from the rapid clay sedimentation. Total influx of carbonized fragments declines in both basins and, though mechanical abrasion prevents insight in Sacnab, the influx of large fragments increases in Quexil. These may be natural and related to climate or purely agricultural possibly resulting from utilization of savanna areas. If agricultural, one may infer that burning continues to play a part, though a decreasing one, in agricultural methods. As a general technique, one can well understand how burning at this stage might not be desirable. Whereas previously the cutting and burning of deep-rooted vegetation had the net effect of restoring nutrients to the surface soil where they could be utilized by shallow-rooted crops, here the apparent lack of deep-rooted vegetation would indicate that the downward leaching of nutrients to deeper soil levels during a cropping period rendered those nutrients lost to future agriculture. Further, the clay sedimentation in both lakes indicates that erosion or soil creep was a major problem for agriculturalists. Both forms of nutrient loss from agricultural areas would make the losses resulting from burning such as combustion products and blown or washed ash, relatively more important than previously. Under these conditions the use of a mulch which might prevent surface erosion and allow a slower release of nutrients would be preferred in

most areas to burning. Exceptions would be savannas and any other low grass areas which would produce the large carbonized fragments observed. By the time of the collapse, the lack of large fragments indicates that no such areas remained and that the Gramineae present existed as scattered opportunists.

The record during the Classic and subsequent periods is similar to that found for the Lake Peténxil basin. An exact comparison is difficult due to differences in identification and counting technique and the representation of the pollen as a percentage of the total arboreal pollen in Peténxil.

The characteristics of the sediments change dramatically at the 230 cm level in Quexil with a sudden lack of coarse macrofossils, a change from coarse gyttja to gyttja, lower C/N ratios, lower total C and total N, and increased density of Ostracods, Pediastrum and small Gastropods. Typha increases and is consistently present from this point on as is Potamogeton.

In Sacnab, sediment is altered to clay with lenses of lower clay content which appear related to the snail layers in Quexil. From 205 cm to the beginning of the Post-Maya period, Quexil sediments are mainly clay-gyttja. These changes cannot be accounted for solely by the increasing land use demonstrated by the pollen. While the presence of clay is doubtless due to disturbance and upland erosion, the suddenness of the change to clay in Sacnab and the presence of the lenses of lower clay content suggest that initially the cause may not have been so direct especially when one considers that the major point-source of clay in this basin is the seasonal stream in the northeast shore draining bajo areas which would act as a buffer on allochthonous clay.

The change to gyttja in Quexil at this point suggests increased lake level and this is consistent with the aquatic fossils present. The lower C/N ratio indicates that sediment from a littoral bog area was not being transported to the coring site, yet the snail layers at 220-225 cm and in the clay-gyttja section at 185 and 200 cm which are also levels of increased Typha influx, do suggest temporary periods of lower levels and littoral proximity. Increased total rainfall would account for the deeper lake level and, by increasing the rate of flow through bajo areas, the sudden change to clay sediment in Sacnab. Temporary decreases in total rainfall would then explain the snail layers and the layers of lower clay content in Sacnab. Any such explanation must explain the difference between these snail layers and the layers of coarse macrofossils at 290-350 cm with the hypothetically equivalent clay lenses in Sacnab. These were hypothesized to be due to either maximal degree of seasonality leading to transport of sediment from a littoral bog area and clay transport through the bajo areas under a more intense rainy season or increased rainfall under a highly seasonal regime. Two independent sources of variation may be observed to parallel these variations in sediment. Neither of these sources varies to a degree that could be considered significant in itself, but the observed co-variation makes some interpretation possible though not certain. The first is the influx of large carbonized fragments which in the 230-350 cm section may be observed to be low in the presence of coarse macrofossils and high otherwise while in the 180-230 cm section high influx is found in the shell layers, with low influx between.

This variation corresponds with that to be observed in the relative pollen diagram between the minor peaks of Gramineae and Cecropia, Gramineae peaks occurring in the shell layers but between the macrofossil layers and Cecropia the reverse. These may represent generalized successional trends or succession on a specific type of area: there is little enough evidence to infer the existence of variation but none to fully explain its source. The association of this variation with that for large fragments influx and snail layers is, however, consistent with a pattern of variation in total rainfall and, in following this pattern back to the macrofossil layers, one may infer that these layers represent periods of high rainfall with the results differing from the later period because of a highly seasonal climate. Under highly seasonal conditions, lake levels would alter seasonally to an extent which caused a littoral bog area rather than a stable littoral zone. Under such circumstances some sediment from this area would reach the coring site during the rainy season but the coarser material would only be transported under conditions of higher rainfall which would also result in less local burning and an increased likelihood of Cecropia succession rather than Gramineae. Such higher rainfall would also result in clay reaching the Sacnab coring site. The sudden Moraceae increase at 320 cm in Quexil and 520 cm in Sacnab would therefore represent a short period of less intensive seasonality.

The section around 250 cm in Quexil appears to be transitional, as previously hypothesized, with low rainfall though less seasonal than previously and is followed by a shift to conditions of higher rainfall and low seasonality. This shift would also allow for a higher net

productivity in land use and make exploitation of savanna areas a profitable proposition. Previous comments on the tenuous nature of climatic evidence still apply.

From the time of the Maya collapse to Spanish incursion, the archeological record remains fragmentary and, perhaps more important, indicates that local social and population changes did not occur in any systematic manner. Inferences drawn from the pollen and sedimentary evidence must therefore be largely suggestive.

The decline in *Ambrosia* from the 170 cm level to the 140 cm level is marked by increasing *Trema*, *Cecropia* and *Urticales* as well as the beginning of reforestation indicated by increasing *Moraceae* and "Other AP". *Compositae* and disturbance indicators decrease as does *Gramineae*, the latter indicating, as previously hypothesized, that it exists as a scattered opportunist rather than any grassland area. The only thing which is surprising in this is that the Collapse is gradual in this non-urbanized area as opposed to the apparent suddenness well documented in urban areas. As previously mentioned, *Ambrosia* in the Petén is an indicator of active human disturbance and its gradual decline can only be representative of the gradual dispersal of the local population. At the 140 cm level influx of total carbonized fragments and large carbonized fragments increase and may indicate renewed agriculture once population reaches its lowest level but if so, it is not clear why such efforts did not commence earlier when reforestation indicates less pressure on land use. This may be related to a lack of nutrients in the surface soil.

Conditions in the Sacnab basin were similar in terms of reforestation but here the Ambrosiae curve does not decline to the same extent. This may indicate that population dispersal was more complete in previously more densely populated areas but the presence of such a large population in the Sacnab basin during this period is in direct conflict with the archeological evidence. Either the population persisted in the use of Classic style ceramics in which case their presence might be overlooked or an interim level in the Sacnab core (e.g., 190 cm) would show a lower level of Ambrosiae equivalent to that found at 140 cm in Quexil. In any case, it is clear that in both basins populations declined gradually after the collapse but that occupation was continuous.

The period of low population between Classic and Postclassic shows a decline in clay deposition in Sacnab but in Quexil this period is marked by a series of laminations. Ostracods, Gastropods, Botryococcus and Pollen/cc, being expressed as density, all show a sharp decline which indicates a high sedimentation rate and/or a high rate of diagenesis while peaks of Total C and in particular Total P occur. The C/N ratio is high. The meaning of these laminations is unclear though possibly related to a decline of clay erosion resulting in a burst of lake productivity through decreased turbidity. There does not appear to be any equivalent in the Lake Peténxil study so it must simply be considered an interesting feature which might well repay closer study.

Expansion of Postclassic population in both basins results in increased clay deposition and slight decreases in forest. Ambrosiae, Compositae and other indicators of disturbance increase while Trema

and Cecropia decrease. Urticales increases as does Gramineae. In Quexil total carbonized fragment influx initially increases but declines through the Postclassic while the influx of large fragments increases and maintains a high level subsequently. In Sacnab there is little change in carbonized fragment influx. All of these trends are reversed during an apparent hiatus in population growth at the 110-120 cm level of Quexil but continue subsequently. This hiatus is not apparent in the Sacnab basin though it simply may have been missed due to the long intervals between samples.

Disturbance appears to be a continuation of the pattern observed during the Classic Maya period. Despite indications of reforestation which may be regional, continuous disturbance of all areas within the basin is indicated not so much by the pollen present, as by the pollen which is not present. The almost explosive increases in pollen of forests, successional stages and bank associations observed after the final population decline at 85 cm in Quexil suggest that during the Postclassic local land use was intensive. These Post-Mayan expansions are so extraordinary that one might suspect them to be an artifact of an underestimated age for the 85 cm level were they not also to be observed in the relative diagram though sharply attenuated by the increasing Moraceae.

The local maintenance of levels of land use intensity during the Postclassic which were comparable to the Classic suggests a number of important features. Whatever reason there was for the formation of such a nuclear settlement pattern as observed at Topoxté, it was also sufficient to cause nucleation of exploited areas if we assume, as thus

far believed, that populations were minimal or non-existent in potentially exploitable areas away from these basins. Though hunting may have been practiced in such areas, the suggested land use intensity indicates agriculture was not.

This implies that the level of land use intensity practiced during the Classic period was not so undesirable or so much of a strain to the agriculturalists or so unstable as one might have believed. While during that period a greater proportion of local productivity would have gone to support local and distant non-agricultural persons thus bringing a measure of discontent into the lives of local agriculturalists, the point is that during the Postclassic, when the social conditions were completely altered, a comparable level of land use intensity was maintained. Admittedly this occurred under the evident pressure for nucleation and it may represent close to the highest level of land use intensity possible for this area, yet it suggests that forced agricultural intensification and environmental degeneration may not have been the system pathology which was instrumental in causing the collapse. This maintenance of intensification along with the slow dispersal of non-urban post-collapse populations strongly indicate that the collapse was a social phenomenon brought about by factors such as class separation, social rigidity or lack of inspirational leadership though the circumstance which acted as a trigger remains unknown.

The minor peaks of Gramineae between 80 cm and 120 cm in Quexil are associated with slight increases in Byrsonima, Quercus and Quercoid pollen as well as shell layers, Typha increases and increased influx

of large carbonized fragments. As previously, these suggest incidence of lower rainfall and lake levels, the latter also observed in the Peténxil analysis.

Final population dispersal leads not only to rapid reforestation but also increases in all forms of vegetation to the extent that one might consider all modern vegetation to be post-Mayan. Maximum reforestation as indicated by the Moraceae took approximately 150 years. Though disturbance has been continuous, it has been more intensive during the most recent century during which time savanna to the south of Lake Quexil was re-established. Land use patterns appear similar to those observed for the earliest Maya, with increases in Cecropia, Urticales and "Other AP" though one difference is declining rather than increasing Moraceae.

In Sacnab, population decline resulted in decreasing clay sedimentation, the slow decrease relative to that in Quexil being due to the buffering action of the bajo area, and reforestation as seen in Quexil. There are however fewer indications of modern disturbance except the slight decline in Moraceae and increase in "Other AP" at the 10 cm level which indicates the recent period when there was a village between the lakes. Bajo AP increases during the post-Maya period but its greatest increase is in the most recent sediments.

Aside from the three incidents of low rainfall during the Post-classic and early post-Maya periods there are no definite indications of climatic alteration during the past 1200 years. The earliest portion of the climatic record resembles the general pattern observed elsewhere in the tropics while that for later periods, in particular

the period 1200-3000 BP, does so only superficially. Though the local climatic record indicates possible alterations in the location of the sub-tropical highs and the general strength of circulation, any extrapolation to major climatic processes must depend on the future availability of comparable records from lowland sites at slightly different latitudes. Yucatan and Honduras or Nicaragua suggest themselves.

One major difficulty with this record is that the type of past climatic alteration is indicated but not the extent making comparison with modern climate difficult beyond the coarse comparisons possible through lake levels. Whereas vegetational changes generally give a clearer indication of the extent of climatic alterations, here the extent expressed is roughly proportional to the extent of disturbance, varying from proportionality with the specific nature and area of such disturbance. It would therefore be desirable to have a comparable record from an historically undisturbed site in this area which would allow the extent of alteration to be estimated against the natural resistance of vegetation. This seems unlikely to be found in the Petén though records where human disturbance has been quantifiably different may suffice.

It may still be stated with some confidence that the Maya formative periods were periods of greater-than-present climatic variation particularly with regard to rainfall. In that the success of tropical agriculture depends to a critical degree on the prediction of the annual rainfall pattern, an anthropologically naive paleoecologist may be forgiven for idly suggesting that a period of such disquieting variability might serve as a necessary crucible and impetus for that

pattern of social accretion and differentiation which produces a social structure central to which is a religion attempting to control nature's uncertainties.

SUMMARY

As a part of the project "Historical Ecology of the Maya Area", this dissertation attempts to examine the pollen and plant fossils in the Holocene sediments of two lakes in the Petén lakes region of Guatemala and relate the observations to what is known of lowland Maya history, local population growth and distribution, climatic sequences in the lowland tropics and the nature of tropical vegetation. The irreducible unit of study is assumed to be one of which terrestrial, aquatic, climatic and human social systems are intimately interlocked components such that the states and processes of any one may affect the others.

The Petén is a low lying karst area within which the depressions of an east-west trending fault line at 17° north latitude have become the Petén lake chain composed of 13 lakes together with a number of aguadas and sinkholes. Sediments analyzed for this dissertation were obtained in Lake Quexil near the present island city of Flores and in Lake Sacnab, 45 km to the east and one of a pair of similar and adjacent lakes within the Yaxha-Sacnab basin. Both lakes are mesotrophic, of internal drainage and bounded to the north by an escarpment. The Lake Quexil basin lacks swampy bajo areas but has a savanna on the flat area of moderately friable silty clay to the south of the lake whereas Lake Sacnab, bounded to the south by hills, has a bajo area to the immediate northeast.

In contrast to the lateritic soils under forest and savanna in the flatter southern Petén, the hilly lakes area exhibits a juxtaposition between the young, well drained and easily leached Black Calcareous Lithosols under high forest on slopes and the deep, poorly drained, plastic clay Hydromorphic soils of the low-lying bajos. Between these extremes are found the fertile Calcimorphic Rendzina soils on rolling areas and gentle slopes.

Climate is warm and humid with a mean average annual temperature of 25.5°C and an average annual rainfall of 1600 mm only 5 to 10 per cent of which falls in the 5 months (January-May) of the dry season. As a result, surface drainage is inconsistent and the many streams are seasonal.

The typical vegetation on well drained slopes is a diverse, broad-leaved, three-storied mesophytic forest which may exhibit a degree of deciduousness according to variations in rainfall. Vegetation in the bajo areas varies from wet grassland to dense swamp thicket and swamp forest according to topography and related flooding. On lower slopes and rolling areas a gradient of forest vegetation exists characterized by palms and the more adaptable high forest and bajo constituents. Beyond a range of karst hills to the south of the lakes are found a more xerophytic flat-land forest and areas of open savanna with occasional fire-resistant arboreal species. Climate, soils and vegetation are suitable for slash-and-burn agriculture, the modern staples being maize and beans.

Archeological records of the earliest sedentary populations in the area are found in Northern Belize at the Cuello site where an Early Preclassic phase from 2500 to 1300 BC has been observed. Middle Preclassic populations were apparently more widespread and composed of small villages of agriculturalists exploiting forest and riverine resources. Archeological investigation of the Yaxha-Sacnab basin demonstrate a density of 24.9 persons/km² by the end of the Middle Preclassic (250 BC) with residences located on higher terrain, the development of 3 distinct socio-political zones and the presence of specialized structures for ceremonial or civic functions. Population within the basin grew exponentially at a rate of 0.17 per cent per year from this period through the Late Classic period (880 AD, density 210.5 persons/km²). Throughout this time there was a continued preference for high terrain and an increasingly complex society developed as indicated by an increasing number of minor centers, complex residential configurations, palace structures and the emergence of the center of Yaxha as truly dominant in the area. Land shortages were probably felt at some point during the Late Preclassic (250 BC - 250 AD), by the end of which population within the basin had reached a density of 60.6 persons/km², resulting in agricultural and land-use intensification. For unknown reasons, population density in the Yaxha-Sacnab basin, as elsewhere, fell precipitously during the Terminal Classic period (post 880 AD) to 21.6 persons/km².

After a hiatus of unknown duration, a nucleated Postclassic population was established on the islands of Topoxté in Lake Yaxha with density on the islands estimated at 11,762 persons/km² and a total

population for the basin of 5,000 persons. Topoxté is thought to have been abandoned prior to 1525 when the Spanish first contacted the Postclassic Itza capital of Tayasal believed to have been at or near Flores. The Spanish conquest of the Itza and population dispersal took place in 1697.

Analysis of the sediments of Lake Peténxil, adjacent to Lake Quexil shows maximum local extent of savanna to have occurred between 4000 and 1400 ^{14}C years BP, dating being subject to an unknown degree of carbonate error. Subsequent Maya disturbance resulted in alterations in sediment chemistry, pollen and aquatic fossils but no indications of significant climatic change (aside from lake level changes), disastrous increases in erosion rates or serious population pressure were observed. One conclusion was that local Mayan populations had in some manner caused a grassland to be turned into a high forest.

Holocene climatic sequences for lowland tropical areas which might assist in the interpretation of observations in the Petén are highly variable. Common features of sequences between Florida and Panama indicate the initial filling of karst lakes around 8000 BP as a result of rising sea-level, drier and/or more seasonal conditions than today between 8000 and 4500 years BP and a climate similar to today's subsequently. Differences between sequences, though possibly indicative of the process of climatic change, may result from dating errors, differences in technique and interpretation, human disturbance of vegetation or the changing configurations of Caribbean currents and sea-surface temperatures.

Sequences from tropical Africa are more numerous and commonly show humid periods between 10000 and 7500 years BP and between 6500 and 5000 years BP. A dry period around 3000 years BP is often, though not universally indicated.

Tropical climatic sequences have been more confidently inferred from the dating of lake level changes and formation of dunes than from palynology. This may result from the limited representation of tropical vegetation in fossil pollen and a lack of understanding of the processes of vegetational change. These considerations lead to the conclusion that pollen alone is inadequate for interpretation of historical processes in tropical areas and that any paleoecological hypothesis must have as its basis consistency with as many forms of stratigraphic evidence as can be made available. One such form of evidence used in this dissertation is the changing amounts and types of carbonized plant fragments in the sediments, interpretation of which is predicated on the observation that they are predominately Gramineae cuticles. Assuming that burning grasses give rise to fairly consistent proportions of the various fragment sizes, the size spectrum at any given sediment level may be used as an indicator of source distance except where there is reason to believe no grasses were burning.

Cores were obtained with a 1-1/2" Livingstone corer in 7.2 meters of water in Lake Quexil and in 7.5 meters of water in Lake Sacnab. The bathymetry of Lake Quexil is such that the core site might have been in an isolated pond should lake level have been sufficiently lower in the past. Cores were transported in their tubes to the

Florida State Museum where processing and analysis were performed using established methods. An exception is that pollen were counted under high magnification (750 x) and dark phase contrast in order to facilitate observation and differentiation of the many small pollen types.

The sediments of all lakes observed in this area contain a layer of silty clay dating from the Classic and Postclassic periods, the thickness of which is related to the extent of local Mayan disturbance. Stratigraphy of the 630 cm Lake Sacnab core shows such a layer with layers of gyttja above and below it. Lenses of increased clay content occur in the lower gyttja layer while lenses of increased gyttja content occur towards the bottom of the clay layer. Bottom sediments of the 650 cm Lake Quexil core suggest bajo-like soil with initial filling of the lake associated with a high content of coarse plant material. Among this plant material was a large wood fragment used for a carbonate error-free ^{14}C date (8410 ± 180 ^{14}C years BP). Subsequent alterations between coarse and fine gyttja may be indicative of shallow and deep-water conditions or incidents of sediment redeposition.

From 350 to 230 cm there is an increasing content of coarse plant material. At 230 cm sediment changes to gyttja, then clay-gyttja at 205 cm and gyttja at 85 cm. Shell layers occur in the areas of these changes.

Initial pollen analysis shows that the Quexil core penetrated sediments of greater age than the Peténxil core and that prior to the grassland observed at the bottom of the latter, high forest dominated

the local vegetation. Indications of human disturbance are observed from the 530 cm level upwards. Comparison of the records of pollen, aquatic fossils and sediment type make it unlikely that all observed changes were solely due to human disturbance.

The use of higher magnification and larger pollen sums results in improved insight into vegetational changes. The most impressive feature of local environmental history was the extent of Mayan deforestation but details, particularly of the grassland maximum, are complicated by the percentage dominance of Moraceae and Urticales pollen. Observed changes could be largely mathematical artifacts. Pollen in the clay layers of the Sacnab core were subject to post-depositional abrasion and destruction but the pollen stratigraphy closely resembles and can be related to that for the Quexil core. Differences are believed to represent changes in present-day savanna as opposed to present-day bajo areas which in the Pre-Mayan period appear to have resembled a mosaic of ponds, banks and grasslands. Specific interpretation of the Sacnab core is difficult but it functions as a reference for the differentiation of regional and local changes in the Quexil core.

With the exception of the bottom-most date in Quexil, ^{14}C dates are all subject to an unknown and apparently inconsistent degree of carbonate error. Dating control for the preparation of a pollen influx diagram is therefore based on features of local Mayan history. Resulting pollen influxes are averaged by use of a running mean to compensate for short-term changes in the conditions and rates of sedimentation as well as mathematical inaccuracies. Post-depositional

destruction of pollen in the clay layers is not indicated in the Quexil core though it is in Sacnab. Destruction of aquatic fossils may occur in both. The bottom of the Sacnab core is estimated to be equivalent to the 510 cm level in Quexil.

Changes in the sediment and aquatic fossils in the Pre-Mayan section of the Quexil core indicate a pattern of lake level changes similar to that derived for the tropics generally based on lake levels and dune formation. Data on pollen and carbonized fragment influx suggest a more complex climatic pattern but are insufficient to demand modification of the general interpretation of periods of humidity at 10000 - 7500 BP and 6500 - 5000 BP. Above 530 cm (5000 BP) vegetation is assumed to be subject to exponentially increasing human disturbance.

Initial disturbance and resultant savannaization of the area south of Lake Quexil appears to have re-enforced a preference for higher terrain. The period 3000 - 5000 BP was one of increasing disturbance of upland areas in both basins resulting in an increasing dominance of Moraceae within existing forest, possibly due to the effect of the prevailing climate on early successional dynamics. If so, this might indicate a change from evergreen to semi-deciduous forest and along with changes in the aquatic plant pollen and the C/N ratio of the sediments, suggests a climate that was more seasonal or drier than that previously.

The period 1500 - 3000 BP, which includes the 1800 BP savanna maximum, is the most difficult to interpret. Climatic alteration and increasing population apparently resulted in shifting patterns of

of land use and vegetation both of which increased in diversity over the whole area as a result of both becoming increasingly specific to the features of any one site. The period was one of increasing climatic variability under a highly seasonal regime. Such variability may have been due to between year variation in seasonality or total rainfall and appears to reach a maximum between 2000 and 2800 BP. The period 1500 - 2000 BP appears to be one of decreased seasonality but lower total rainfall and lake levels resulting in impenetrable sediments at the Peténxil coring site, the possible existence of the deeper-water Quexil coring site in a separate pond and, in combination with land pressure and the related nature of human disturbance, maximum spread of savanna in the area.

While the climatic changes affect lake levels and littoral vegetation directly, their effect on vegetation during this period is less straightforward since their point of impact is the successional stages. The vegetational expression of climate was therefore primarily a function of the specific nature and location of human disturbance. Continued preference for upland areas in both basins is indicated throughout this period and, lacking indications of decreasing fallow cycles, this may have involved continuous exploitation. As land pressure forced utilization of less preferred areas, climate was such that savanna on flatter areas and possibly low deciduous forest on lower slopes and rolling areas resulted. Vegetational, as well as climatic and lacustrine interpretation may, however, be contaminated in underestimated or unknown ways by the apparent general conditions of instability.

Around 1500 BP climate altered to a pattern which has apparently persisted to today. Seasonality decreased relative to the previous periods and total rainfall and lake levels increased. Subsequent incidents of lower lake levels are indicated by shell layers and decreases in the pollen of aquatic plants in the Quexil core.

During the Classic period all indicators of primary and secondary forest decline steadily to the point of almost non-existence. *Ambrosia* increases exponentially while other indicators of disturbance are continuously present. In the Lake Sacnab basin, *Moraceae* persists at a higher percentage which may indicate lower population density and less intensive land use than near Lake Quexil. Savanna declines in a way which suggests human utilization or physical occupation. Erosion and/or soil creep increase in both basins and burning appears to play less of a role in agriculture except possibly in the exploitation of savanna areas. By the time of the Collapse almost all areas in the Quexil basin and to a lesser extent in the Sacnab basin were subject to permanent use.

Population dispersal was gradual in the non-urbanized Quexil basin as opposed to the apparent suddenness well documented in urban areas. Over a period of about 25 years *Ambrosia* and disturbance indicators decline steadily as successional species increase and reforestation begins. Conditions in the Sacnab basin were similar in terms of reforestation but the *Ambrosia* curve does not decline to the same extent. While this might indicate a larger residual population, it may result from the larger sampling interval. Both basins were continuously occupied at low population levels through the hiatus

during which time clay content of the sediments declines as a result of decreased erosion or increased lake productivities.

Expansion of Postclassic populations in both basins results in increased clay deposition and indicators of disturbance. Pollen of primary and secondary forest species decrease. An hiatus in Postclassic population growth occurs at 400 BP in Quexil but growth continues subsequently to population dispersal at 270 BP. This hiatus would have occurred around the time of and may be related to initial Spanish contact. A major feature of Postclassic populations is that the level of local land use intensity was similar to that during the Classic period. This suggests that both Postclassic settlements and agriculture were highly nucleated. It further suggests that the level of land use intensity practiced during the Classic period, while perhaps close to the maximum attainable, may not have been a direct cause of the Collapse. This maintenance of intensification along with the observed slow dispersal of non-urban post-Collapse populations strongly indicate that the Collapse was a social phenomenon centered in urban areas.

Final population dispersal leads not only to rapid reforestation but also increases in all forms of vegetation to the extent that one might consider all modern vegetation to be post-Mayan. Maximum reforestation as indicated by the Moraceae took approximately 150 years. Although Post-Maya disturbance has been locally continuous, it has been more intensive during the most recent century during which time savanna to the south of Lake Quexil has been re-established.

The climatic record for the Petén lakes resembles the pattern observed elsewhere in the tropics though it only does so superficially during the 1200 - 3000 BP period. Comparable records from lowland sites at slightly different latitudes in Mesoamerica may allow extrapolation of the results to major climatic processes. The record indicates the type of past climatic changes but the relative extent of change is indicated by the degree of vegetational change which is roughly proportional to the extent of disturbance. It would therefore be desirable to have a comparable record from an historically undisturbed site in this area which would allow the extent of alteration to be estimated against the natural resistance of vegetation.

It is submitted that any hypothesis regarding social change amongst the Maya must fully consider the effects and interactions of climatic, vegetational and lacustrine alterations.

LITERATURE CITED

- Bartlett, A.S. and E.S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate and sea-level change). In A. Graham (ed.) *Vegetation and Vegetational History of Northern Latin America*. Elsevier Scientific, New York.
- Beard, J.S. 1944. Climax vegetation in tropical America. *Ecology*, Vol. 25: 125-158.
- Beard, J.S. 1953. The savanna vegetation of northern tropical America. *Ecological Monographs*, Vol. 23: 149-215.
- Bourliere, F. and M. Hadley. 1970. The ecology of tropical savannas. *Annual Review of Ecology and Systematics*, Vol. 1. Annual Reviews, Palo Alto, California.
- Bowler, J.M., G.S. Hope, J.N. Jennings, G. Singh, and D. Walker. 1976. Late Quaternary climates of Australia and New Guinea. *Quaternary Research*, Vol. 6: 359-394.
- Brenner, M. 1978. Paleolimnological assessment of human disturbance in the drainage basins of three northern Guatemalan lakes. Unpublished Master's thesis, Department of Zoology, University of Florida, Gainesville.
- Brezonik, P.L. and J.L. Fox. 1974. The limnology of selected Guatemalan lakes. *Hydrobiologia*, Vol. 45: 467-487.
- Bronson, B. 1966. Roots and the subsistence of the ancient Maya. *Southwestern Journal of Anthropology*, Vol. 22: 251-279.
- Budowski, G. 1961. Tropical savannas, a sequence of forest felling and repeated burnings. *Turrialba*, Vol. 6: 23-33.
- Bullard, W.R. 1960. Maya settlement patterns in Northeastern Petén, Guatemala. *American Antiquity*, Vol. 25: 355-372.
- Bullard, W.R. 1971. Topoxté, a Postclassic Maya site in Petén, Guatemala. In Bullard (ed.), *Monographs and Papers in Maya Archeology*. Peabody Museum of Archeology and Ethnology, Papers, Vol. 61. Harvard University, Cambridge.
- Bullard, W.R. 1973. Postclassic culture in Central Petén and adjacent British Honduras. In Culbert (ed.), *The Classic Maya Collapse*. University of New Mexico Press, Albuquerque.

- Butzer, K.W., G.L. Isaac, J.L. Richardson, and C. Washburn-Kamau. 1972. Radiocarbon dating of East African lake levels. *Science*, Vol. 175: 1069-1076.
- Butzer, K.W., R. Stuckenrath, A.J. Bruzewicz, and D.M. Helgren. 1978. Late Cenozoic paleoclimates of the Gaap Escarpment, Kalahari margin, South Africa. *Quaternary Research*, Vol. 10: 310-339.
- Chase, A. 1976. Topoxté and Tayasal: ethno-history in archeology. *American Antiquity*, Vol. 41: 318-334.
- Clausen, C.J., A.D. Cohen, C. Emiliani, J.A. Holman, and J.J. Stipp. 1979. Little Salt Spring, Florida: a unique underwater site. *Science*, Vol. 203: 609-614.
- Colinvaux, P.A. 1972. Climate and the Galapagos Islands. *Nature*, Vol. 240: 17-20.
- Conklin, H.C. 1957. Shifting cultivation and succession to grassland climax. *Proceedings of the Ninth Pacific Science Congress*, Vol. 7: 60-62.
- Covich, A. 1976. Recent changes in molluscan species diversity of a large tropical lake (Lago de Petén, Guatemala). *Limnology and Oceanography*, Vol. 21: 51-59.
- Covich, A. and M. Stuiver. 1974. Changes in Oxygen 18 as a measure of long-term fluctuations in tropical lake levels and molluscan populations. *Limnology and Oceanography*, Vol. 19: 682-691.
- Cowgill, U.M. 1961. Soil fertility and the ancient Maya. *Transactions of the Connecticut Academy of Arts and Sciences*, Vol. 42: 1-56.
- Cowgill, U.M. and G.E. Hutchinson. 1963. El Bajo de Santa Fe. *Transactions of the American Philosophical Society, New Series* 53, Part 7.
- Cowgill, U.M., G.E. Hutchinson, A.A. Racek, C.E. Goulden, R. Patrick, and M. Tsukada. 1966. The history of Laguna de Peténxil, a small lake in northern Guatemala. *Memoirs of the Connecticut Academy of Arts and Sciences*. Vol. XVII.
- Culbert, T.P. 1973a. *The classic Maya Collapse*. University of New Mexico Press, Albuquerque.
- Culbert, T.P. 1973b. The Maya downfall at Tikal. *In* Culbert (ed.), *The Classic Maya Collapse*. University of New Mexico Press, Albuquerque.

- Deevey, E.S. 1978. Holocene forests and Maya disturbance near Lake Quexil, Petén, Guatemala. *Pol. Arch. Hydrobiol.* Vol. 25: 117-129.
- Deevey, E.S., M. Brenner, S. Flannery, and G.H. Yezdani. 1979. Lakes Yaxha and Sacnab, Petén, Guatemala: limnology and hydrology. *Archiv. Hydrobiol.* in press.
- Deevey, E.S., G.B. Deevey, and M. Brenner. 1979. Structure of the zooplankton communities in the Petén lake district, Guatemala. In Kerfoot (ed.). *The Evolution and Ecology of Zooplankton Communities*, ASLO Special Symposium 3. University of New England Press, Hanover, New Hampshire.
- Deevey, E.S., D.S. Rice, M. Brenner, and S.J. Flannery. 1978. Classic Maya impact on a lacustrine environment. Paper presented at 1978 SAA meeting, Tucson, Arizona. mimeo.
- Deevey, E.S., D.S. Rice, H.H. Vaughan, M. Brenner, and M.J. Flannery. 1979. Mayan urbanism: impact on a tropical karst environment. in press.
- Deevey, E.S. and M. Stuiver. 1964. Distribution of natural isotopes of carbon in Linsley Pond and other New England lakes. *Limnology and Oceanography*, Vol. 9: 1-11.
- Deevey, E.S., H.H. Vaughan, and G.B. Deevey. 1977. Lakes Yaxha and Sacnab, Petén, Guatemala: Planktonic fossils and sediment focusing. In Golterman (ed.). *Interactions between Sediments and Fresh Water*. Proceedings of an International Symposium held at Amsterdam, The Netherlands, Sept. 6-10, 1976. Dr. W. Junk B.V. Publishers, Wageningen.
- Denslow, J.S. 1978. Mechanisms of succession in tropical rainforest - a contribution from Mexico. *Ecology*, Vol. 59: 862.
- Ewel, J. and R. Myers. 1974. Preliminary vegetation studies at Yaxha, Guatemala. (unpublished)
- Flint, R.F. 1971. *Glacial and Quaternary Geology*. John Wiley and Sons, New York.
- Gomez-Pompa, A. 1973. Ecology of the vegetation of Veracruz. In Graham (ed.) *Vegetation and Vegetational History of Northern Latin America*. Elsevier Scientific, New York.
- Gomez-Pompa, A., S. del Amo R., C. Vazquez-Yanes, and A. Butando C. 1976. Investigaciones sobre la regeneracion de selvas atlas en Veracruz, Mexico. Cia Editorial Continental, S.A., Calz. de Tlalpan Num. 4620, Mexico, 22, D.F.

- Goodrich, C. and H. Van der Schalie. 1937. Mollusca of Petén and North Alta Vera Paz, Guatemala. Miscellaneous publication 34. University of Michigan, Museum of Zoology, Ann Arbor.
- Green, D.G. 1976. Nova Scotian forest history - evidence from statistical analysis of pollen data. Ph.D. dissertation, Department of Biology, Dalhousie University, Halifax, Nova Scotia.
- Hammond, N., D. Pring, R. Wilk, S. Donaghey, F.P. Saul, E.S. Wing, A.V. Miller, and L.W. Feldman. 1979. The earliest lowland Maya Definition of the Swasey phase. *American Antiquity*, Vol. 44: 92-109.
- Harrison, P.D. 1977. The rise of the bajos and the fall of the Maya. In Hammond (ed.) *Social Processes in Maya Prehistory*. Academic Press.
- Haviland, W.A. 1965. Prehistoric settlement at Tikal, Guatemala. *Expedition*, Vol. 7: 14-23.
- Haviland, W.A. 1969. A new population estimate for Tikal, Guatemala. *American Antiquity*, Vol. 34: 429-433.
- Haviland, W.A. 1972. Family size, prehistoric population estimates and the ancient Maya. *American Antiquity*, Vol. 37: 135-139.
- Johannessen, C.L. 1963. Savannas of interior Honduras. *IBERO - Americana*: 46. University of California, Berkeley.
- Kellman, M.C. 1974. The viable weed seed content of some tropical agricultural soils. *Journal of Applied Ecology*, Vol. 11: 669-678.
- Kellman, M.C. 1979. Soil enrichment by neo-tropical savanna trees. *Journal of Ecology*, Vol. 67: in press.
- Livingstone, D.A. 1975. Late Quaternary climatic change in Africa. *Annual Review of Ecology and Systematics*, Vol. 6: 249-280.
- Lundell, C.L. 1937. The vegetation of Petén. Carnegie Institution of Washington, Washington, D.C.
- Lundell, C.L. 1938. Plants probably utilized by the Old Empire Maya of Petén and adjacent lowlands. *Papers of the Michigan Academy of Science, Arts and Letters*, Vol. 24.1: 37-56.
- Maler, T. 1910. Explorations in the Department of Petén, Guatemala and adjacent regions: Motul de San José, Petén-Itza. Reports of explorations for the Museum. *Memoirs of the Peabody Museum of Archeology and Ethnology*, Harvard University, Vol. 4, No. 3.

- Maley, J. 1973. Mécanisme des changements climatiques aux basses latitudes. *Paleogeography, Paleoclimatology, Paleoecology*, Vol. 14: 193-228.
- Means, P.A. 1917. History of the Spanish conquest of Yucatan and of the Itzas. Papers of the Peabody Museum of Archeology and Ethnology, VII.
- Namias, J. 1963. Interactions of circulation and weather between hemispheres. *Monthly Weather Review*, Vol. 91: 482-486.
- Namias, J. 1972. Influence of northern hemisphere general circulation on drought in northeast Brazil. *Tellus*, Vol. XXIV: 336-343.
- Nye, P.H. and D.J. Greenland. 1960. The soil under Shifting Cultivation. Technical Communication No. 51, Commonwealth Bureau of Soils, Harpenden.
- Ogden, J.G. and W.C. Hart. 1977. Dalhousie natural radiocarbon measurements, II. *Radiocarbon*, Vol. 19: 392.
- Puleston, D.E. 1968. Brosimum alicastrum as a subsistence alternative for the Classic Maya of the Central Southern Lowlands. Unpublished Masters thesis. Department of Anthropology, University of Pennsylvania, Philadelphia.
- Puleston, D.E. 1974. Intersite areas in the vicinity of Tikal and Uaxactun. In Hammond (ed.), *Mesoamerican Archeology*, University of Texas Press, Austin.
- Puleston, D.E. and O.S. Puleston. 1971. An ecological approach to the origins of Maya civilization. *Archeology*, Vol. 24: 430-446.
- Puleston, O.S. and D.E. Puleston. 1974. A processual model for the rise of Classic Maya civilization in the Southern Lowlands. 40th International Congress of Americanists, Vol. 1: 119-124.
- Reina, R.E. 1967. Milpas and milperos. *American Anthropologist*, Vol. 69: 1-20.
- Rice, D.S. 1976a. The historical ecology of Lakes Yaxha and Sacnab, El Petén, Guatemala. Ph.D. dissertation, Department of Anthropology, Pennsylvania State University.
- Rice, D.S. 1976b. Middle Preclassic Maya settlement in the central Maya Lowlands. *Journal of Field Archeology*, Vol. 3: 425-445.
- Rice, D.S. 1978. Population growth and subsistence alternatives in a tropical lacustrine environment. In Harrison and Turner (eds.), *Prehispanic Maya Agriculture*. University of New Mexico Press, Albuquerque.

- Rice, D.S. and P.M. Rice. 1979. The northeast Petén revisited. *American Antiquity*, in press.
- Richardson, J.L. and A.E. Richardson. 1972. History of an African rift lake and its climatic implications. *Ecological Monographs*, Vol. 42: 499-534.
- Rosy, R.L. 1931. The ethno-botany of the Maya. Tulane University, Middle American Research Series, No. 2: 1-359.
- Sanders, W.T. 1973. The cultural ecology of the Lowland Maya: a re-evaluation. In Culbert (ed.), *The Classic Maya Collapse*. University of New Mexico Press, Albuquerque.
- Sarnthein, M. 1978. Sand deserts during glacial maximum and climatic optimum. *Nature*, Vol. 272: 43-46.
- Simmons, C.S., J. Tareno, and J. Pinto. 1959. Clasificación de Reconocimiento de los Suelos de la República de Guatemala. Instituto Agropecuario Nacional, Servicio Cooperativa Inter-Americana de Agricultura. Ministerio de Agricultura, Guatemala.
- Stevens, R.L. 1964. The soils of Middle America and their relation to Indian peoples and cultures. In West (ed.), *Natural Environment and Early Cultures*. Handbook of Middle American Indians, Vol. 1: 265-315. University of Texas Press, Austin.
- Street, F.A. and A.T. Grove. 1976. Environmental and climatic implications of late Quaternary lake-level fluctuations in Africa. *Nature*, Vol. 261: 385-390.
- Swain, A.M. 1973. A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. *Quaternary Research*, Vol. 3: 383-396.
- Tsukada, M. 1963. Pollen morphology and identification. 1. *Eucosmopollenites*. *Pollen et Spores*, Vol. 5: 239-284.
- Tsukada, M. 1964a. Pollen morphology and identification. 2. *Cac-taceae*. *Pollen et Spores*, Vol. 6: 45-84.
- Tsukada, M. 1964b. Pollen morphology and identification. 3. Modern and fossil tropical pollen with emphasis on *Bombacaceae*. *Pollen et Spores*, Vol. 6: 393-462.
- Tsukada, M. 1966. The pollen sequence. In Cowgill, Hutchinson, Rasek, Goulden, Patrick, and Tsukada (eds.), *The history of Laguna de Peténxil, a small lake in northern Guatemala*. Memoirs of the Connecticut Academy of Arts and Sciences, Vol. XVII.

- Tsukada, M. and E.S. Deevey. 1967. Pollen analyses from four lakes in the southern Maya area of Guatemala and El Salvador. In Cushing and Wright (eds.), Quaternary Paleoecology. Yale University Press, New Haven.
- Tsukada, M. and J. Rowley. 1964. Identification of modern and fossil maize pollen. Grana Palynologica, Vol. 5: 406-412.
- Uhl, C. 1978. Early successional dynamics after a cut and burn treatment on tropical lateritic soils. Bulletin of the Ecological Society of America, Vol. 59: 114. (abstract)
- Viniegra O., F. 1971. Age and evolution of salt basins of south-eastern Mexico. American Association of Petroleum Geologists Bulletin, Vol. 55: 478-494.
- Vinson, G.L. 1962. Upper Cretaceous and Tertiary stratigraphy of Guatemala. American Association of Petroleum Geologists Bulletin, Vol. 46: 425-457.
- Vivo Escoto, J.A. 1964. Weather and climate of Mexico and Central America. In West (ed.), Natural Environment and Early Cultures, Handbook of Middle American Indians, Vol. 1. University of Texas Press, Austin.
- Waddington, J.C.B. 1969. A stratigraphic record of the pollen influx to a lake in the Big Woods of Minnesota. Geological Society of America, Special Paper 123: 263-282.
- Wagner, P. 1964. Natural vegetation of Middle America. In West (ed.), Natural Environment and Early Cultures, Handbook of Middle American Indians, Vol. 1. University of Texas Press, Austin.
- Watts, W.A. 1969. A pollen diagram from Mud Lake, Marion County, northcentral Florida. Geological Society of America Bulletin, Vol. 80: 631-642.
- Watts, W.A. 1971. Postglacial and interglacial vegetation history of southern Georgia and central Florida. Ecology, Vol. 52: 676-690.
- Webster, D. 1975. Warfare and the evolution of Maya civilization. Paper presented at the Conference on Maya Origins, Santa Fe.
- Webster, P.J. and N.A. Streten. 1978. Late Quaternary Ice Age climates of tropical Australasia: interpretations and reconstructions. Quaternary Research, Vol. 10: 279-309.
- West, R.C. 1964. Surface configuration and associated geology of Middle America. In West (ed.), Natural Environment and Early Cultures, Handbook of Middle American Indians, Vol. 1. University of Texas Press, Austin.

- Wilken, G.C. 1971. Food producing systems available to the ancient Maya. *American Antiquity*, Vol. 36: 432-438.
- Willey, G.R. 1975. The rise of Maya civilization: a summary view. Paper presented at the Conference on Maya Origins, Santa Fe.
- Willey, G.R. and W.R. Bullard. 1965. Prehistoric settlement patterns in the Maya Lowlands. In Willey (ed.), *Archeology of Southern Mesoamerica*, Vol. 1, *Handbook of Middle American Indians*, Vol. 2. University of Texas Press, Austin.
- Wymstra, T.A. and T. Van der Hammen. 1966. Palynological data on the history of tropical savannas in northern South America. *Leidse Geologische Mededelingen*, Vol. 38: 71-90.

APPENDIX A

INITIAL ANALYSES OF LAKE QUEXIL CORE 1
PERFORMED BY G.H. YEZDANI AND H. VAUGHAN

Figure 11: Lake Quexil Core 1: Relative Pollen Diagram: Arboreal

ARBOREAL POLLEN DIAGRAM



Figure 12: Lake Quexil Core 1: Relative Pollen Diagram: Nonarboreal

LAKE QUEXIL, PETEN, GUATEMALA -

- NON-ARBOREAL POLLEN

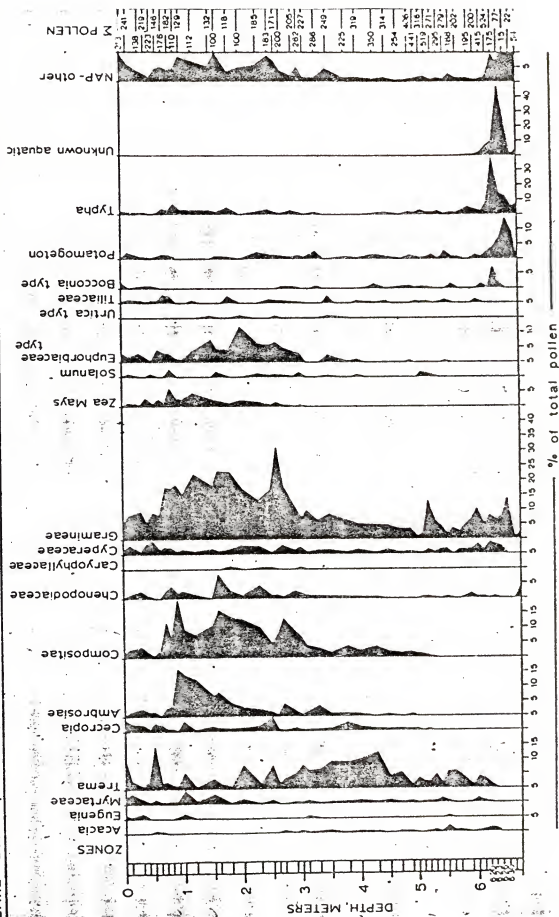


Figure 13: Lake Quexil Core 1: Sponge Spicule and Rhizopod Density

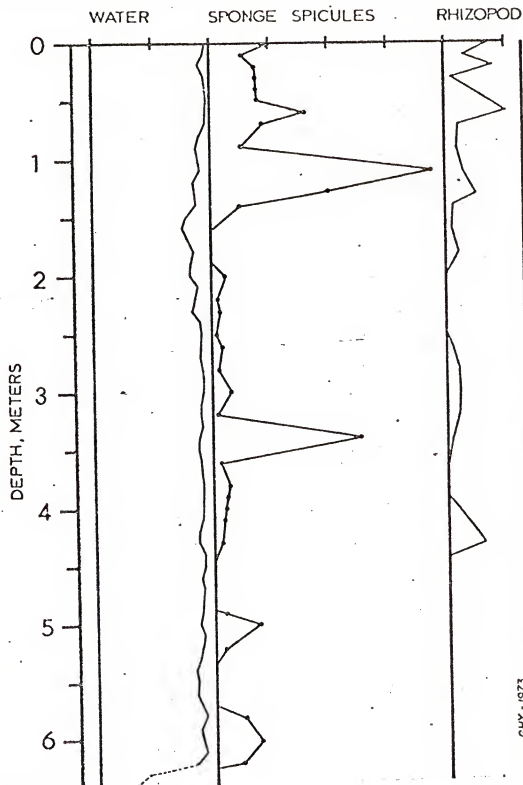


Figure 14: Lake Quexil Core 1: Phytoplankton Density

LAKE QUEXIL, Peten, GUATEMALA.

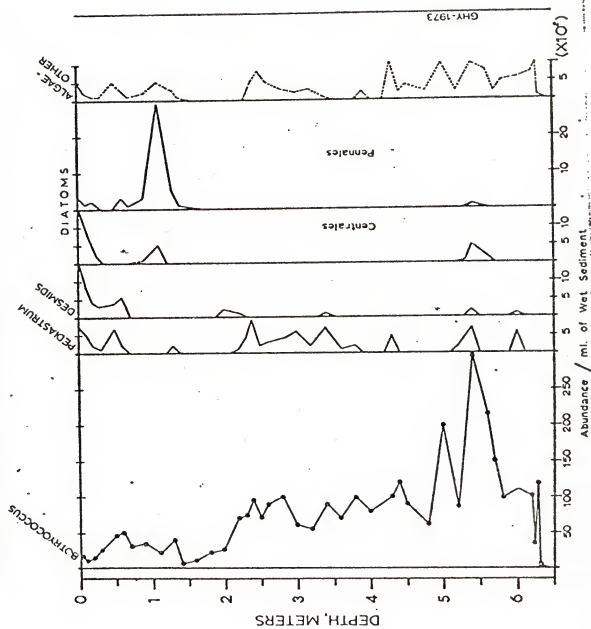


Figure 15: Lake Quexil Core 1: Zooplankton Density

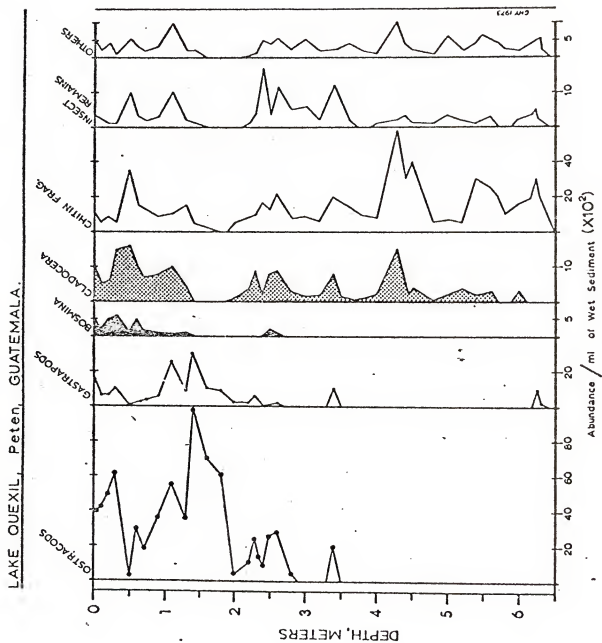
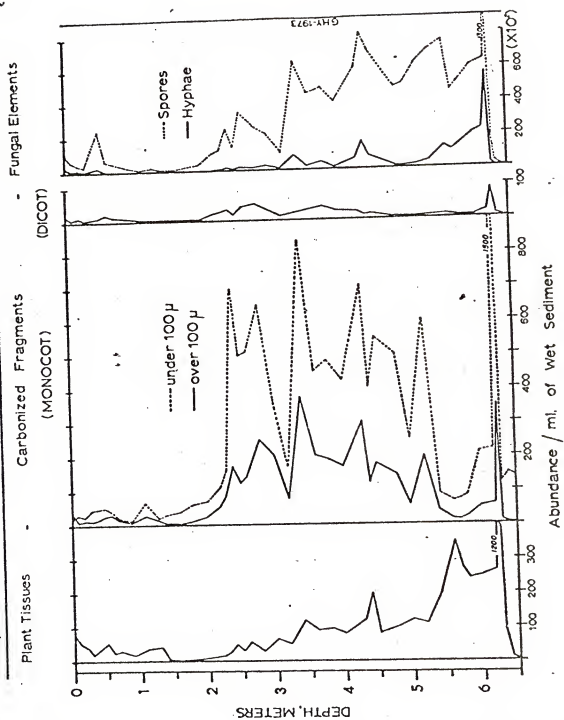


Figure 16: Lake Qexil Core 1: Plant Tissue, Carbonized Fragment
and Fungal Element Density

LAKE QUEXIL, Peten, GUATEMALA.



APPENDIX B

EXAMPLE CALCULATIONS

At each sediment level, two types of sample treatment were used in this analysis: one in which the sediment sample was processed for pollen and another which was deflocculated only and to which was added a known amount of Lycopodium pollen

1) Pollen processed slide

Assume that 100 grains of arboreal species A, 50 grains of non-arboreal species B and 25 grains of aquatic species C were observed on the slide. At the same time 100, 40 and 60 non-pollen fossils X, Y and Z were observed.

For the relative pollen diagram (Figures 5 and 6):

The Pollen Sum	=	150 grains	
Per cent of A	=	$\frac{100 \text{ grains}}{150 \text{ grains}}$	= 66.6
Per cent of B	=	$\frac{50 \text{ grains}}{150 \text{ grains}}$	= 33.3
Per cent of C	=	$\frac{25 \text{ grains}}{150 \text{ grains}}$	= 16.6

2) Deflocculated slide

Assume that 50,000 Lycopodium grains were added to .5 cc of original sediment. Observed on the slide were 500 grains of Lycopodium, 1,000 μ^2 total of carbonized fragments, 10 grains of species A, 6 of species B, and non-pollen fossils X, Y and Z in amounts of 9, 5 and 5.

The amount of sediment within which these fossils were observed would be:

$$\frac{500 \text{ grains}}{50,000 \text{ grains}} \times .5 \text{ cc} = .005 \text{ cc}$$

Carbonized fragment density of the sediment would be:

$$\frac{1,000 \mu^2}{.005 \text{ cc}} = 200,000 \mu^2/\text{cc} \quad (\text{Figures 5 and 6})$$

The conversion factor to be applied to the pollen sum would be the mean of:

$$\frac{10 \text{ grains A}}{100 \text{ grains A}} = .1$$

$$\frac{6 \text{ grains B}}{50 \text{ grains B}} = .12$$

$$\frac{9 \text{ of X}}{100 \text{ of X}} = .09$$

$$\frac{5 \text{ of Y}}{40 \text{ of Y}} = .125$$

$$\frac{5 \text{ of Z}}{60 \text{ of Z}} = .083$$

$$\text{Mean factor} = .104$$

Pollen density of the sediment for those types which were included in the pollen sum would be:

$$\frac{.104}{.005 \text{ cc}} \times 150 \text{ grains} = 3120 \text{ grains/cc} \quad (\text{Figure 8})$$

If the sedimentation rate derived for this section of the core were .1 cm/yr.:

Total carbonized fragment influx would be:

$$200,000 \mu^2/\text{cc} \times .1 \text{ cm/yr} = 20,000 \mu^2/\text{cm}^2/\text{yr}. \quad (\text{Figure 9})$$

Total pollen influx of those species included in the pollen sum would be:

$$3120 \text{ grains/cc} \times .1 \text{ cm/yr} = 312 \text{ grains/cm}^2/\text{yr}. \quad (\text{Figure 9})$$

If the pollen influx for the level immediately above this one were 320 grains/cm²/yr and that for the level immediately below were 306 grains/cm²/yr, the averaged pollen influx for this level would be:

$$\frac{320 + 312 + 306}{3} = 312.\dot{6} \text{ grains/cm}^2/\text{yr.} \quad (\text{Figure 9})$$

The influx of the different pollen types would then be:

$$\text{A: } 66.\dot{6}\% \times 312.\dot{6} = 208.6 \text{ grains/cm}^2/\text{yr.}$$

$$\text{B: } 33.\dot{3}\% \times 312.\dot{6} = 104.1 \text{ grains/cm}^2/\text{yr.}$$

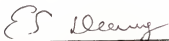
$$\text{C: } 16.\dot{6}\% \times 312.\dot{6} = 52.2 \text{ grains/cm}^2/\text{yr.}$$

(Figure 10)

BIOGRAPHICAL SKETCH

Hague Hingston Vaughan was born on July 3, 1948, in Montreal. He attended Lower Canada College in Montreal, earning his senior matriculation in 1966. He acquired his undergraduate education at Dalhousie University in Halifax, Nova Scotia, majoring in Biology with a minor in Chemistry and received a Bachelor of Science degree with Honours in 1970. Commencing graduate work at Dalhousie, Mr. Vaughan transferred to the Department of Zoology, University of Florida in 1971. In 1976 and 1977 he was a faculty member of the University of Maine in Orono teaching Limnology, Paleoecology and Pollen Analysis. He resides at present in Montreal.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



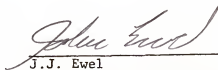
E.S. Deevey, Chairman
Graduate Research Professor of Zoology and
Graduate Research Curator, Museum

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



F.G. Nordlie
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



J.J. Ewel
Associate Professor of Botany

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1979

Dean, Graduate School